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The Social and Ecological Dimensions of Vertebrate Management: Reintroductions and Invasions

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Environmental Science and Management

by

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Hiroyasu, E.H.T., Miljanich, Christopher, Anderson, Sarah E. Attitudes and Grizzly bear reintroduction in California. *Human Dimensions of Wildlife*, 24(5). DOI: 10.1080/10871209.2019.1622055.

Hiroyasu, E.H.T. and J.J. Hellmann. Invasive species and Climate Change. *Biodiversity and Climate Change: Transforming the Biosphere.* Thomas E. Lovejoy and Lee Hannah (Eds.). New Haven, CT: Yale University Press.

Imbach, Pablo, P. Serra-Diaz, L. Hannah, E. Fung, and **E.H.T. Hiroyasu**. 2019. Modeling species and vegetation distribution under climate change. In *Biodiversity and Climate Change: Transforming the Biosphere*. Thomas E. Lovejoy and Lee Hannah (Eds.). New Haven, CT: Yale University Press.

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Hiroyasu, E.H.T., C.P. Miljanich, S.E. Anderson. Rewilding California: How values, knowledge, and salience shape wildlife management. Presented at 2017

Pathways Conference on Human Wildlife Dimensions. 18-20 September 2017; Estes Park, CO.

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Christie, JC, E. DeMarco, **E.H.T. Hiroyasu**, A. Kreger, M. Ludington. (2014). The status of wild pigs (Sus scrofa) in the state of California and on Tejon Ranch. Poster session presented at: International Wild Pig Management Conference. 13-15 April 2014; Montgomery, AL.

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ABSTRACT

The Social and Ecological Dimensions of Vertebrate Management: Reintroductions and Invasions

by

Elizabeth H.T. Hiroyasu

Conflicts between wildlife and humans continue to be a persistent problem across a wide spectrum of landscapes. In the body of work below, I focus on two classes of vertebrates in particular, invasive pest species and reintroduced species. Invasive species and reintroduced species are both species with which humans can conflict, which has profound consequences for the persistence of species across the landscape and long term human livelihoods. Populations of both invasive and native species typically exist at low densities at first, then establish, grow, and spread across the landscape. Both invasions and reintroductions can be strongly influenced by the human landscape and tolerance for the presence of particular species and their associated impacts to nature and their livelihoods. For invasive and pest species, opposition to eradication programs has the ability to stop or stall management, which has implications for the successful establishment and spread of an invasive species. Conversely, public support or opposition for reintroduction programs can dictate whether they happen at all. Understanding the human landscape of tolerance is important in understanding the success or failure of conservation programs more generally.

The body of work below focuses on both of these classes of species and examines different problems associated with each, using techniques from both natural and social sciences.

The first three chapters of this dissertation focus on the ecological and social dynamics of vertebrate pest species. I begin by exploring the utility of barn owls to reduce and control populations of vertebrate pests in agricultural landscapes. Next, I examined case of the wild pig, first comparing the population demographic characteristics of wild pigs and second, understanding what kinds of message frames can increase support for invasive wild pig management. Finally, I used social science techniques to understand attitudes toward grizzly bear reintroduction in California.

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INTRODUCTION

Human-wildlife conflicts arise when wildlife on the landscape impact human occupancy or livelihoods. Such conflicts can have negative impacts on both wildlife, through retaliatory killing or persecution; and on humans, through property damage, losses in agricultural production, or direct threats of bodily injuries (Nyhus, 2016). As a result, solving problems related to human-wildlife conflict requires tackling both human and wildlife aspects.

In the body of work below, I focus on two situations where human-wildlife conflicts can arise, species invasions and species reintroductions. In many ways, the ecological dynamics of invasive species (considered an "environmental bad" that needs to be controlled) and reintroduced species (an "environmental good" that helps with the conservation of desirable or endangered species) are very similar. Invasive and reintroduced populations both typically exist at low densities at first, then establish, grow, and spread across the landscape (Williamson & Fitter, 1996). But establishment, growth, and spread are strongly influenced by the human landscape, particularly tolerance for the presence of wildlife species and their associated impacts to nature and their livelihoods (Carter & Linnell, 2016).

Instead of the binary economic and ecological impacts that conservationists often cite in human-wildlife interactions, an understanding that public attitudes can range along a continuum from "conflict" to "appreciation" needs to be reflected in approaches to conservation and management of wildlife. For invasive and pest species, opposition to eradication programs can stall or stop implementation of management programs (Bremner & Park, 2007), which has implications for the successful establishment and spread of an invasive species. Conversely, public support for or opposition to reintroduction programs can dictate whether introductions happen at all (Dunham, White, Allen, Marcot, & Shively, 2016), which can leave landscapes absent of species that fill important ecological and cultural roles. Understanding the human

landscape of tolerance is therefore important in understanding the success or failure of conservation programs (for both invasive and native species) more generally. Meanwhile, the life history and ecology of the species itself also determines human ability to manage or coexist with it. Highly intelligent species that learn to navigate the human landscape like brown and black bears can incite fear for bodily injury or forage on livestock species. Alternatively, pest species like rodents can reproduce quickly and have large impacts in agricultural settings. Using techniques from ecology and social science, I seek to understand how to better manage human-wildlife conflicts that occur across a human-dominated landscape.

Invasive and Pest Species

Invasive species are species that are not native to the environment in which they have become established, and that cause harm to humans or the environment (Executive Order No. 13112, 1993; United Nations, 1992). Pest species also cause economic harm or harm to human health, but they are not necessarily nonnative to the ecosystem in which they are causing harm. Invasive species can have stronger, and indeed novel, impacts on a system when compared to native pest species, because the system (both its human and ecological aspects) is not adapted to their presence.

Invasive species have been identified as one of the most important drivers of environmental change and declines in global biodiversity (Chapin et al., 2000; Early et al., 2016; M. C. Mack & D'Antonio, 1998). Almost half of endangered species in the US are at risk as a result of invasive species presence and impacts (Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998). From an economic perspective, invasive species impacts are estimated to result in $120 billion annually in management and damage costs (Pimentel, Zuniga, & Morrison, 2005). However, there is an uneven distribution of costs and benefits of control programs that alleviate the impacts of invasive species (Finnoff, McIntosh, Shogren, Sims, & Warziniack, 2010), which

can make it difficult to motivate public support for invasive species management policies. Invasive species management is further complicated by the fact that methods such as poisoning, shooting, or release of other species to mitigate invasive species impacts (or eradicate the species altogether) often have high up-front costs, can have unintended ecological consequences, and can be socially polarizing (R. N. Mack et al., 2000).

Reintroduced Species

Reintroduced species are those that have been added back to a landscape from which they have been extirpated, typically to restore some kind of ecosystem function or help safeguard the species from global extinction (Seddon, Armstrong, & Maloney, 2007). Despite the fact that reintroductions vary greatly in their success, interest in reintroducing wildlife to landscapes has been increasing in recent years (Dunham et al., 2016). It is often difficult to predict the impacts that a species will have on the landscape into which it is reintroduced; such changes are especially likely to affect people who may no longer be accustomed to a species' presence on the landscape. Reintroducing species to any landscape is likely to result in innumerable challenges; from unexpected influences on important ecosystem services relied upon by local human populations, to increased and unregulated human interactions with the species in question. These potential conflicts ultimately dictate the long-term success or failure of reintroduction endeavors.

Even before species ever re-enter a landscape via reintroduction, reintroduction proposals can be highly controversial. For example, wolf reintroduction in the Greater Yellowstone Ecosystem was hotly debated for 18 years before their successful reintroduction in 1995 because of concerns about the threats that wolves posed to ranching operations and recreationalists in the area (Bath, 1989). In the Bitterroot mountains in Montana and Idaho, public opposition to grizzly bear (*Ursus arctos horribilis*) reintroduction to connect populations was

so strong that the project was halted (Interagency Grizzly Bear Committee, n.d.). Just like with invasions, public support or opposition to reintroduction efforts can dictate the outcome. One way to promote coexistence and mitigate conflicts is to understand the public's opinions about reintroduction programs and what drives those opinions.

Chapter Overviews

The first three chapters of this dissertation focus on the ecological and social dynamics of vertebrate pest species, both native and invasive. I first explored the use of barn owls (*Tyto alba*) as a biocontrol for vertebrate rodent pests, pocket gophers (*Thomomys* spp.) and voles (*Microtus* spp.). Vole and pocket gopher populations have significant impacts on California agricultural systems (Baldwin, Salmon, Schmidt, & Timm, 2014), and barn owls have been proposed as a part of broader integrated pest management plans. However, the efficacy of barn owls to control and reduce rodent pest populations is not well understood (Kross & Baldwin, 2016). Using predator-prey models, I estimated when we can expect biocontrols to succeed in reducing conflict between humans and rodent pest species.

The second and third chapters of this dissertation focus on invasive wild pigs (*Sus scrofa*) and their associated management. Wild pigs have significant impacts on agricultural and natural systems across both their native and invasive ranges (Barrios-Garcia & Ballari, 2012). Despite this, eradication programs are costly and have been controversial in some of the places they have been carried out (PETA, 2011). In the second chapter, I examined the differences in population demographic characteristics between populations of wild pigs (*Sus scrofa*) in the native range and invaded ranges, to understand how populations in the native range can inform better management in the invasive range. The third chapter used a social science approach and examined the use of message frames to increase public support of wild pig eradication programs.

Taken together, these two chapters represent a broad interdisciplinary approach to wild pig management.

Finally, the fourth and last chapter examined the human-wildlife conflicts that arise from species reintroductions, using a similar approach as the third chapter to understand public opinion related to species reintroductions. Given that reintroduction programs require public support to move forward, we sought to understand the factors that drive support for a species reintroduction, focusing on the case of the grizzly bear in California. Together, these chapters provide lessons for how to best manage wildlife in a human-dominated landscape.

CHAPTER I:

MULTIPLE STABLE STATES WHEN EMPLOYING A GENERALIST PREDATOR BIOCONTROL.

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Abstract:

Agricultural pests and invasive species are persistent problems for land managers worldwide, and billions of dollars are spent every year in an attempt to suppress populations of detrimental species. While chemical pesticides are widely used, land managers are increasingly incorporating natural predators of pest species into their Integrated Pest Management (IPM) strategies. However, limited research has focused on the underlying predator-prey dynamics of natural enemy, generalist biocontrols, especially for vertebrate pests. Using a predator-prey model, we explored the effectiveness of using generalist predators that are not numerically responsive to prey densities. We modeled both a Type-II or Type-III prey functional response. Using dimensional analysis we demonstrate that equilibrium prey density is determined by three scaled parameters: the ratio of predator density to prey carrying capacity, the inverse of predator efficiency times carrying capacity, and the constant q. We identified all equilibria and performed local stability analysis. We performed a bifurcation analysis to determine how the existence and stability of these equilibria varied across parameter space. We found that, depending on predator abundance and efficiency, the model can exhibit stable equilibria at high prey abundance, low or zero prey abundance, or both, with bistability occurring at biologically realistic parameter values. The primary effect of the functional response type (other than mathematical tractability) was

whether the "effective biocontrol" equilibrium was represented by prey extinction (Type II) or prey persistence at low densities (Type III). To demonstrate the application of these models to a particular pest management problem, we parameterized the models using data on barn owls (*Tyto alba*) preying on pocket gophers (*Thomomys* spp.) and voles (*Microtus* spp.) in California agricultural fields, a widespread IPM tactic worldwide. These findings suggest that generalist predators can be an effective tool in IPM strategies, but their success depends on both the predator density and the efficiency of the predator being introduced. Careful accounting of the dynamics of the target prey species can ensure the effectiveness of biocontrols.

Introduction

The management of vertebrate and insect pests is an enduring challenge across all types of managed landscapes. Extensive use of pesticides is widespread, and rising concerns about their primary and secondary effects have spurred the increased popularity of Integrated Pest Management (IPM) programs (Christensen, Lassen, and Elmeros 2012; Gabriel et al. 2012). IPM strategies are one way to reduce pesticide use across the landscape by minimizing pest populations through a variety of techniques including biocontrol and cultural practices (Engeman and Witmer 2000); but in order to be effective IPM requires a detailed understanding of the interactions between pests and their natural enemies. Biocontrols, species that can increase the mortality rate of a target pest species, are a commonly used tool in IPM to reduce the abundance, density, survivorship, or performance of pest species (Stiling and Cornelissen 2005), and there is extensive literature exploring the effectiveness of biocontrol agents, particularly in agricultural systems (Fagan et al. 2002; Stiling and Cornelissen 2005; Symondson, Sunderland, and Greenstone 2002). Classically, biocontrol development has focused on specialist predators (including herbivores) or parasitoids (Symondson, Sunderland, and Greenstone 2002) because of concerns about unintended consequences such as non-target impacts by the

introduced agent (Stiling and Cornelissen 2005). While such concerns are often warranted, there may be settings where generalist predators are an effective part of an IPM strategy.

Generalist predators differ from specialists in that they are not limited by the availability of a single type of prey. Instead, they are limited by the total abundance of prey or other environmental variables such as habitat availability. Debates surrounding the efficacy of generalist versus specialist predators are ongoing, and failures of generalist predator introductions have caused managers and the public to shy away from them (see Howarth 1991; Stiling and Cornelissen 2005; Symondson, Sunderland, and Greenstone 2002 for review). Additionally, evidence supporting the effectiveness of generalist predators at suppressing pest species is mixed; in their meta-analysis of biocontrols, Stiling and Cornelissen (2005) found that generalists did not outperform specialists, while Jandricic et al. (2016) found that pest control under a generalist aphid depended on crop cycle and plant development. Despite this, generalist predators are an attractive option for IPM because they can target multiple common pest species by switching prey depending on availability and a diversity of pest species can support higher predator densities (Messelink et al. 2010). Ecological studies suggest that generalist predators may have a stabilizing effect on rodent population cycling in natural landscapes (Hanski, Hansson, and Henttonen 1991).

To extend our knowledge of the effectiveness of generalist biocontrols, we turned to ecological models to guide our intuition and determine the effectiveness of establishing generalist predators for control of agricultural pests. Standard predator-prey models assume that predators are specialists, limited by the abundance of the focal prey species, displaying a "numerical response" in which predator populations grow when prey are abundant and decline when prey are rare. In contrast, predator-prey models that include generalists, which are polyphagous or exhibit prey switching, are particularly difficult to model because of the number

of parameters required, including the role of predator preferences, and shifts in prey densities over time (Symondson, Sunderland, and Greenstone 2002).

Here, we extend our understanding of generalist predator-prey dynamics and focus on situations where the producer can directly control the predator abundance, either indirectly through the provision of non-prey limiting resources (such as habitat features) or directly through release of predator individuals (such as predatory insects in greenhouses). To model this, we retain the dynamic effect of predators on their prey, but change the predator abundance from a dynamic state variable to an externally controlled parameter. Ludwig et al. (1978) applied this approach to the Spruce-budworm and forest system to understand the dynamics of Spruce-budworm outbreaks and declines, and found that there are multiple stable states of Spruce-budworms because of differences between the fast and slow dynamics of the spruce-budworms, generalist bird predators, and forest habitat. Similarly, our model assumes density dependence in the prey and a predator consumption rate that saturates as prey density increases. We extend the Ludwig approach by modelling both the Type II and Type III functional responses; the latter is typically used to describe the dynamics of generalist predators (Holling 1959), but is less mathematically tractable. We use bifurcation theory to assess the stability and equilibria of prey populations and to determine parameter combinations where stable coexistence between the predator and prey species exists, thus identifying when pest populations persist across the landscape despite the introduction of a predator. Collectively, the use of these predator-prey models should identify if, and under what circumstances, generalist predators could potentially be effective biocontrols for pest species in managed landscapes, ultimately allowing for more focused field studies that will be easier to design and implement.

Case Study: Barn owls and rodent pests

To extend our understanding of the effectiveness of generalist predators as biocontrols, we apply our approach to examine the use of barn owls (*Tyto alba*) to control rodent pests in agricultural landscapes. Barn owls are a popular biocontrol agent in agricultural landscapes because the associated costs of establishment and maintenance are relatively low compared to other management options like rodenticides (Browning, Cleckler, and Johnson 2016). Despite their popularity, there is mixed evidence that barn owls are effective at reducing pest population densities and their associated impacts (Labuschagne et al. 2016). A number of studies have measured rodent densities under varying barn owl densities (Duckett and Karuppiah 1990; Chia, Lim, and Buckle 1995; Ho and Teh 1997; Hafidzi and Mohd 2003; Ojwang and Oguge 2003). Some studies have also assessed the relationship between damage associated with rodent pests and barn owl nest box density (Ojwang and Oguge 2003; Browning, Cleckler, and Johnson 2016). However, none of these studies use a replicated design and all occur over relatively short periods of time (<6 months). Additionally, none of the studies empirically quantified barn owl feeding rates on rodent pests and associated reductions in rodent pest densities due to predation. In California, several studies have documented the diet of barn owls (Clark and Wise 1974; Van Vuren, Moore, and Ingels 1998; Kross, Bourbour, and Martinico 2016), but no replicated field studies have simultaneously collected data on owls and the population dynamics of rodent crop pests (but see Browning, Cleckler, and Johnson 2016 for a limited, unreplicated assessment).

Methods

Model

We analyzed a standard predator-prey model with prey density-dependence and nonlinear functional response (Gurney and Nisbet 1998; May 1972; Rosenzweig and MacArthur

1963). However, in keeping with the assumption that the predator density is set by the manager and does not respond numerically to prey density, we treat it as a parameter instead of a state variable:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{cN^{q+1}}{N^{q+1}+D^{q+1}}P \qquad (1)$$

The prey population growth rate depends on the familiar parameters of prey population growth rate (r), prey carrying capacity (K), half saturation constant (D), maximum feeding rate of the predator (c), and predator density (P) (See Table 1 for full parameter definitions and units). The parameter q controls the abruptness with which the predator switches from ignoring the prey to consuming it at the maximum possible rate. A value of $q = 0$ gives a Type II function response and $q = 1$ gives the canonical Type III functional response (Holling 1959, 1965). Any $q > 0$ creates a sigmoid functional response, with the abruptness of the transition from low to maximal feeding rates increasing with q.

Analysis:

We performed dimensional analysis to reduce the parameter set to the minimum number needed to specify the qualitative dynamics. Using the reduced equations, we identified all equilibria and performed local stability analysis. Finally, we performed a bifurcation analysis to determine how the existence and stability of these equilibria varied across parameter space. Bifurcation analysis allowed us to determine if slight changes in parameters resulted in more significant changes in the dynamics of the system. In particular, we were interested in identifying regions of parameter space within which there were multiple stable equilibria (where pest populations might persist over the long term, an undesirable outcome), as well as regions where the prey population may be driven to low density or extinction (the desired outcome). For the

Type II model ($q = 0$) we solved for the bifurcations algebraically (Supplement 1). For the Type III functional response ($q > 0$), it was not possible to solve for the bifurcations algebraically, so we used the numerical continuation package MatCont (Dhooge, Govaerts, and Kuznetsov 2003) in MatLab (r2019a, version 9.6) to solve for the bifurcations (Supplement 2).

Case Study:

To demonstrate the application of these models to a specific pest management problem and understand the biological relevance of our stability analysis, we parameterized the models using data on barn owls preying on pocket gophers (*Thomomys* spp.) and voles (*Microtus* spp.) in California agricultural fields. We chose this case study because barn owls are a popular generalist biocontrol in agricultural systems and are limited by nesting habitat in the form of nest boxes, and not prey availability (Browning, Cleckler, and Johnson 2016). Voles and pocket gophers are well studied rodents with reasonable population growth estimates across a variety of habitats, including in agricultural habitats (for example: voles: Beacham 1979; Krebs 1966; Batzli and Pitelka 1971; pocket gophers: Loeb 1990; Daly and Patton 1986; Howard and Childs 1959). We reviewed the literature on pocket gopher, vole, and barn owl population dynamics to parameterize single-species predator-prey models of barn owl predation. We simulated the predator-prey population dynamics over a five-year time horizon to assess the level of control achieved in a management-relevant amount of time (See Supplement 3 for parameter calculations and simulation results). Finally, we examined the area of parameter space that barn owl, gopher, and vole populations occupied to understand when control in the form of pest extinction or low pest density could be achieved in an agricultural context.

Results

Dimensional Analysis

By rescaling prey abundance, predator abundance, and time, we found that the dynamics of the scaled prey abundance (n) depends only on three parameters: scaled predator density (π), scaled half saturation constant (δ), and the abruptness parameter (q), with the following relationship (Supplemental Information 1):

$$\frac{dN}{d\tau} = n(1-n) - \frac{\pi\, n^{q+1}}{n^{q+1} + \delta^{q+1}} \quad (2)$$

This means that prey abundance depends only on an index of how many predators the manager puts on the landscape, an index of how quickly barn owls can forage and eat rodent pests, and how abruptly owls are satiated. As in the full equations, $q = 0$ represents the Type II functional response and $q > 0$ represents the Type III functional response.

Type II Functional Response: Equilibria and Stability

For the Type II functional response, $q = 0$, so the existence and stability of various equilibria only depend on the scaled half saturation constant (δ) and the scaled predator density (π). Mathematical derivations of the results described below are in Supplement 1.

Figure 1 shows how the scaled predator density (π) affects the number, value, and stability of prey equilibria (n^*), when $\delta = 0.3$. There is always an equilibrium at $n = 0$ (the so-called "trivial" equilibrium), although it is locally unstable for low values of scaled predator density (π). In addition, there may be one or two "non-trivial" equilibria, although one of them may take on negative values, which, while mathematically real, are biologically irrelevant. The figure shows that there are three qualitatively different regions of parameter space, separated by bifurcations. For small values of π, $n = 0$ is unstable and there is only one, relatively large,

positive equilibrium (which is stable); the second nontrivial equilibrium is also stable, but as it is negative it is biologically irrelevant and we can consider the high prey abundance equilibrium to be globally stable. Where the lower nontrivial equilibrium crosses zero, it exchanges stability with the trivial equilibrium via a *transcritical bifurcation.* For intermediate values of π, there is biologically relevant bistability, with both zero and the larger nontrivial equilibria being stable; the domains of attraction of these two equilibria are separated by the unstable lower nontrivial equilibrium. With further increases in π, the two nontrivial equilibria meet and annihilate each other in a *saddle node bifurcation*; at values of π above this point, the zero equilibrium is globally stable.

The same qualitative pattern occurs as long as $\delta < 1$, although the region of bistability shrinks as δ increases. Figure 2 shows four qualitative regions in π-δ parameter space, separated by two curves: a transcritical bifurcation at $\pi=\delta$, and a saddle-node bifurcation at $\pi = \frac{1}{4}(\delta - 1)^2 + \delta$. The three regions described in Figure 1 are labeled IV (positive equilibrium stable), I (bistability), and II (extinction globally stable) in Figure 2. When $\delta > 1$, the saddle-node bifurcation occurs at negative values of the nontrivial equilibria, so the only biologically relevant equilibrium is the trivial equilibrium, which is locally stable. Thus, in region III, like region II, extinction is ecologically globally stable. When $\delta = \pi = 1$, the transcritical and saddle-node bifurcations coincide, creating a pitchfork bifurcation.

Overall, if the scaled predator abundance is sufficiently high, then the prey will be driven to extinction, whereas if it is low, the prey will persist at high densities; this makes clear intuitive sense. In addition, however, if both π and δ are low, then there are two stable states, representing both prey extinction and prey persistence (Figure 2, Area I). Under these circumstances, if the prey is at its single-species equilibrium when the predator is introduced, the

prey abundance will decline somewhat but will not be driven extinct; but if the prey abundance is close to zero (because they have just arrived, or have been reduced by other control measures) when the predator is introduced, then the predator can drive the prey extinct.

Type III Functional Response: Equilibria and Stability

We also conducted equilibria and stability analysis of the trivial and non-trivial equilibria of the Type III functional response, where $q = 1$, which is the traditional parameterization used for generalist predators (Holling 1965). We also varied q here to better understand how the strength of the predator's prey preference might affect the stability and equilibria of the system. Mathematical derivations of the results described below are in Supplement 2.

Unlike the Type II functional response, we found that the trivial equilibrium was always unstable, so the prey cannot be driven extinct; furthermore, there are no negative equilibria. We found that there is always at least one stable, positive equilibrium, which may be very small, so the prey population may be held at a low density. If δ is sufficiently small, then there is a range of values of π in which there are two stable positive equilibria (a high prey abundance and a low prey abundance) separated by an unstable equilibrium (Figure 3). This is analogous to the region of bistability in the Type II model, except that the connection between the unstable equilibrium and the lower equilibrium is via a second saddle node bifurcation, rather than a transcritical bifurcation (Figure 3). At a critical value of δ, the two saddle nodes occur at the same value of P, resulting in a cusp bifurcation. When δ is sufficiently large, there is a smooth (but nonlinear) gradient from high prey abundance to low prey abundance as π increases (Figure S2.2). As q increases, the area of bistability in the $\delta - \pi$ parameter space decreases and the critical value of δ decreases (Figure 4).

Case Study

Supplement 3 shows the output of all the pocket gopher and vole simulations. We found that under the high and medium pocket gopher density scenarios, pocket gopher populations often occurred in area III, the area of noncontrol by the predator (Figure 5a). In contrast, using parameters from the vole simulations show that the low and medium scenarios tend to occur in the stable extinction area (Figure 5b).

Discussion

We found that in the presence of a generalist predator without a numerical response, prey populations depend only on three parameters – scaled predator density (π), scaled half saturation constant (δ), and q. This simplification allows us to more clearly assess local stability and the relationship between parameters and prey populations outcomes. We found that using both the Type II and Type III functional responses with a predator-prey system, multiple stable states may occur when the scaled predator density (π) and scaled half saturation constant (δ) are low. In this circumstance, there can be multiple outcomes to the interaction - either extinction or near extinction of the target prey species or maintenance of the prey population at high abundance. This bistability is important because managers often employ generalist predator species to control pest species, but the success of these programs depends on the area of parameter space that the pest population is in at the time of predator introduction. Managers may be able to push the prey species into a stable extinction phase, but this may require other methods than just implementation of a biocontrol because of limitations to the number of predators that can be stocked. There are two ways that this can be implemented, either by using pesticides to drive the prey below the unstable equilibrium before releasing the predators; or

initially stock sufficiently high predator densities to drive the prey to the low equilibrium, then partially relax the predation pressure by reducing the number of predators on the landscape.

To help make sense of the scaled parameter, in the Type II model, the primary criterion for prey extinction being locally stable is $\pi > \delta$. In the original parameters, this means

$$\frac{Pk_{max}}{D} > r. \qquad (3)$$

The left side is the per-prey death rate due to predation when the prey density is low (when N is close to zero, the denominator of the functional response is close to D). Thus, this says that prey extinction is stable if the low-density predation-induced prey death rate exceeds the low-density prey intrinsic growth rate (r) — which makes biological sense.

Bistability requires (among other things) that δ and π both be less than one. But, how likely is this to occur? $\delta < 1$ means $D < K_{prey}$ – the half-saturation constant of the functional response is less than prey carrying capacity. In other words, if the prey is at carrying capacity, the predation rate by an individual predator is limited more by its ability to process prey than by the prey abundance. Moreover, predators cannot realistically be stocked at an unlimited density, given behavioral constraints. Typically, the half saturation constant is difficult to measure, but for species that we consider to be "pests", we can safely assume that K_{prey} will be "large". This suggests that $\delta < 1$ will often be satisfied in the case of pest species. $\pi < 1$ means that $Pk_{max} < rK_{prey}$. The left side of the inequality represents the total consumption of prey by predators when the prey density is high, while the right side of the inequality is the total intrinsic growth of prey when density is high (at K_{prey}) *if there were no density dependence*. This means that the predation level is not so high that it can control a highly abundant, density-independent population - which is reasonable for the values of r and K_{prey} typically associated with pest species. The area in parameter space of bistability is also affected by the constant q which

characterizes the steepeness of the functional response (Figure 4). A more nuanced understanding of the prey population dynamics is important in determining the effectiveness of the introduced predator and the probability of an undesirable bistable state occurring.

To make sense of the saddle node bifurcation, we can separate the equation into two parts - the intrinsic growth ($rN(1-\frac{N}{K_{prey}})$) and loss due to predation ($\frac{k_{max}N^{q+1}}{N^{q+1}+D^{q+1}}P$). Figure 6 shows both parts as a function of N. The equilibria occur where the two intersect and bistability occurs where the predation curve intersects with the intrinsic growth curve. The saddle-node bifurcation occurs for parameters that cause the two curves to be tangent to each other. There is bistability if the predation pressure is strong enough to suppress the prey population at low density, but not strong enough to overcome the intrinsic population growth when the prey is near $\frac{Kprey}{2}$ (the density that gives maximum total intrinsic population growth). From the modeling perspective, this work dispels a common belief that the Type III functional response is the source of bistability (Murdoch 1969; Spencer and Collie 1996). Any nonlinear functional response that has a negative second derivative at larger values of N will be sufficient to make bistability possible (even if it does not saturate to an asymptote).

The Type II functional response assumes that the target prey species is of high enough value that the predator will search exclusively for that prey item, even when its density is low. However, given that we are evaluating a generalist predator, we expect prey swtiching to occur and captured these dynamics in our assessment of the Type III functional response. Similar to the Type II analysis, we found that there are areas of bistability; however, the stable, lower branch of the equilibrium is greater than zero and the pest population can still persist.

These findings also suggest that past examples of failed generalist biocontrols may not have failed because of the predator's inability to control a pest but rather because of other

parameters such as pest carrying capacity and the maximum feeding rate of the predator. For example, if pest population dynamics occupy the parameter space where only the upper equilibrium is stable, then predators will not be effective at reducing the prey population to low levels. Simulation exercises of predator and prey populations (with Type II growth) show that prey populations can persist in the presence of predators, showing that commonly used densities of owls (0.2 and 0.6 owls/ha) and estimated owl efficiency is not enough to drive rodent populations to the stable, non-trivial extinction state.

Application to Management

This research has some concrete insights for land managers and agriculturalists specifically. First, simple models from classical ecology are relevant to guiding our intuition about how to manage pests. Using models like these as a first pass to characterize the system can be a rapid 'back of the envelope' approach to understand whether or not biocontrols may be effective on a landscape and indicate if other management tools will be needed to develop an effective IPM program. To use this, managers will need to have some knowledge of the density of pests across the landscape and about the foraging behavior of the predator of they plan to implement. Second, we demonstrate that generalist predator biocontrols are a viable component of an IPM program. If the pest population exists in a parameter space where predators may not be effective, additional pest management tools (e.g., cultural practices, traps, pesticides) may be employed to reduce populations to the point where they can then be driven to extinction or a lower equilibrium. Newsome (1990) found this method to be effective for rabbit control in Australia. Finally, these models can be used to inform managers about what density predators should be stocked at to push the system toward the stable state of prey extinction. While we use the example of barn owls, these same principles and findings can be applied to any situation where the density of the predator is determined by the manager - such as insect predators that

are released in a greenhouse, where the insect density is determined by the greenhouse manager. Likewise, this same approach could be used to guide hunting strategies to control invasive species populations, where the hunting effort is determined by managers.

Model limitations and future directions

While this exploration of the relationship between predator and prey is informative, it omits features that could prove important to understanding the role of generalist predators to control pests in agricultural landscapes. In practice, parameters such as half-saturation constant (D) or even carrying capacity (K) may be difficult to measure or estimate. We do not include any effect of environmental stochasticity in this model which may impact both the foraging efficiency of the predator and the population dynamics of the prey population. While the agricultural setting that this research is targeted toward is expected to be somewhat homogenous, incorporating the impacts of seasonality and weather would provide a more realistic assessment of the dynamics. We also assume that the environment is closed and do not account for recruitment in the prey population from immigration, which is possible especially if reductions in the target prey population open more space or resources. In an agricultural setting, re-invasion is likely to occur and managers will need to account for this in their IPM plan. Finally, pest densities can vary significantly depending on crop type and location, and more refined data about population dynamics of pest species will make these models more robust and specific to the landscapes being managed.

For our case study, further research is needed to obtain more precise estimates of the predator-prey dynamics between owls and rodent populations. While there are many studies assessing the diet of barn owls, few have measured the efficiency or search behavior of owls in natural or agricultural settings. Given the sit-and-wait strategy that barn owls employ when foraging, these parameters may be difficult to measure. When more precise parameters are

obtained, a formal bifurcation analysis of the Type-III functional response may provide a more realistic estimate of the effectiveness of barn owls as a management tool as it accounts for prey switching and predator learning. Finally, inclusion of the effect of rodenticides or trapping (as is common in IPM) in the form of a pulsed mortality function will paint a clearer picture of the role of biocontrols as a strategy used in IPM.

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Literature Cited

Batzli, George O., and Frank A. Pitelka. 1971. "Condition and Diet of Cycling Populations of the California Vole, Microtus californicus." *Journal of Mammalogy* 52 (1): 141–63.

Beacham, Terry D. 1979. "Survival in Fluctuating Populations of the Vole Microtus-Townsendii." *Canadian Journal of Zoology* 57 (12): 2375–84. https://doi.org/10.1139/z79-309.

Browning, Mark, John Cleckler, and Matthew Johnson. 2016. "Prey Consumption by a Large Aggregation of Barn Owls in an Agricultural Setting." In *Proc. 27th Vertebr. Pest Conf.*, edited by Robert M. Timm and Roger A. Baldwin, 337–44.

Chia, T.H., J.L. Lim, and A. Buckle. 1995. "Barn owls for rat control on oil palm plantations-Do they work?" *The Planter* 71: 109–17.

Christensen, Thomas Kjær, Pia Lassen, and Morten Elmeros. 2012. "High exposure rates of anticoagulant rodenticides in predatory bird species in intensively managed landscapes in

Denmark." *Archives of Environmental Contamination and Toxicology* 63 (3): 437–44. https://doi.org/10.1007/s00244-012-9771-6.

Clark, J.P., and W.A. Wise. 1974. "Analysis of barn owl pellets from Placer County, California." *The Murrelet* 55 (5-7).

Daly, J. C., and J. L. Patton. 1986. "Growth, Reproduction, and Sexual Dimorphism in Thomomys bottae Pocket Gophers." *Journal of Mammalogy* 67 (2): 256–65. https://doi.org/10.2307/1380878.

Dhooge, A., W. Govaerts, and Yu A. Kuznetsov. 2003. "MATCONT: A MATLAB package for numerical bifurcation analysis of ODEs." *ACM Transactions on Mathematical Software* 29 (2): 141–64. https://doi.org/10.1145/779359.779362.

Duckett, J E, and S Karuppiah. 1990. "A guide to the planter in utilizing barn owls (Tyto alba) as an effective biological control in mature oil palm plantations." In *Proceedings of the 1989 International Palm Oil Development Conference-Agriculture*, edited by S. Jalani, Z.Z. Zin, K. Paranjothy, D. Ariffin, N. Rajanaidu, S.C. Cheah, M.W. Basri, and I. Henson, 357–72.

Engeman, Richard M., and G W Witmer. 2000. "Integrated management tactics for predicting and alleviating pocket gopher (Thomomys spp.) damage to conifer reforestation plantings." *Integrated Pest Management* 5: 41–55.

Fagan, William F., Mark A. Lewis, Michael G. Neubert, and P. Van Den Driessche. 2002. "Invasion theory and biological control." *Ecology Letters* 5 (1): 148–57. https://doi.org/10.1046/j.1461-0248.2002.0 285.x.

Gabriel, Mourad W., Leslie W. Woods, Robert Poppenga, Rick A. Sweitzer, Craig Thompson, Sean M. Matthews, J. Mark Higley, et al. 2012. "Anticoagulant rodenticides on our public and community lands: Spatial distribution of exposure and poisoning of a rare forest carnivore." *PLoS ONE* 7 (7). https://doi.org/10.1371/journal.pone.0040163.

Gurney, W.S.C., and R.M. Nisbet. 1998. *Ecological Dynamics*. 1st ed. New York, NY: Oxford University Press.

Hafidzi, M.N., and NA'IM Mohd. 2003. "The use of the barn owl, Tyto alba, to suppress rat damage in rice fields in Malaysia." In *Rats, Mice, and People: Rodent Biology and Management*, edited by Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs, and Dave M. Spratt. Canberra: Australian Centre for International Agricultural Research.

Hanski, Ilkka, Lennart Hansson, and Heikki Henttonen. 1991. "Specialist Predators, Generalist Predators, and the Microtine Rodent Cycle." *Jounal of Animal Ecology* 60 (1): 353–67.

Ho, Cheng Tuck, and Chong Lay Teh. 1997. "Integrated Pest Management in Plantation Crops in Malaysia: Challenges and Realities." In *Plantation Management for the 21st Century*, 125–50. Kuala Lumpur.

Holling, C.S. 1959. "The Components of Predation as Revealed by a Study of Small Mammal Predation of the European Pine Sawfly." *The Canadian Entomologist* XCI (5): 234–61.

———. 1965. "The Functional Response of Predators to Prey Density and its Role in Mimicry and Population Regulation." *The Memoirs of the Entomological Society of Canada* 97: 5–60.

Howard, W.E., and H.E. Childs. 1959. "Ecology of pocket gophers with emphasis on Thomomys bottae mewa." *Hilgardia* 29: 277–358.

Howarth, F. G. 1991. "Environmental impacts of classical biological control." *Annual Review of Entomology. Vol. 36*, 485–509.

Jandricic, Sarah E., Stephen P. Wraight, Dave R. Gillespie, and John P. Sanderson. 2016. "Biological control outcomes using the generalist aphid predator Aphidoletes aphidimyza under multi-prey conditions." *Insects* 7 (4). https://doi.org/10.3390/insects7040075.

Krebs, Charles J. 1966. "Demographic Changes in Fluctuating Populations of Microtus californicus." *Ecological Monographs* 36: 239–73.

Kross, Sara M., Ryan P. Bourbour, and Breanna L. Martinico. 2016. "Agricultural land use, barn owl diet, and vertebrate pest control implications." *Agriculture, Ecosystems and Environment* 223: 167–74. https://doi.org/10.1016/j.agee.2016.03.002.

Labuschagne, Lushka, Lourens H. Swanepoel, Peter J. Taylor, Steven R. Belmain, and Mark Keith. 2016. "Are avian predators effective biological control agents for rodent pest management in agricultural systems?" *Biological Control* 101: 94–102. https://doi.org/10.1016/j.biocontrol.2016.07.003.

Loeb, Susan C. 1990. "Reproduction and population structure of pocket gophers (Thomomys bottae) from irrigated alfalfa fields." *Proceedings of the Fourteenth Vertebrate Pest Conference 1990*, no. Paper 56.

Ludwig, D., D.D. Jones, and C.S. Holling. 1978. "Qualitative Analysis of Insect Outbreak Systems : The Spruce Budworm and Forest." *Journal of Animal Ecology* 47 (1): 315–32.

May, Robert M. 1972. "Limit cycles in predator-prey communities." *Science* 177 (4052): 900–902. https://doi.org/10.1126/science.177.4052.900.

Messelink, Gerben J., Roos van Maanen, Renata van Holstein-Saj, Maurice W. Sabelis, and Arne Janssen. 2010. "Pest species diversity enhances control of spider mites and whiteflies by a generalist phytoseiid predator." *BioControl* 55 (3): 387–98. https://doi.org/10.1007/s10526-009-9258-1.

Murdoch, William W. 1969. "Switching in General Predators : Experiments on Predator Specificity and Stability of Prey Populations." *Ecological Monographs* 39 (4): 335–54.

Newsome, A. 1990. "The control of vertebrate pests by vertebrate predators." *Trends in Ecology and Evolution* 5 (6): 187–91. https://doi.org/10.1016/0169-5347(90)90208-U.

Ojwang, D O, and N O Oguge. 2003. "Testing a biological control program for rodent management in a maize cropping system in Kenya." In *Rats, Mice, and People: Rodent Biology and Management*, edited by Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs, and Dave M. Spratt, 96:251–53. Canberra: ACIAR.

Rosenzweig, M.L., and R.H. MacArthur. 1963. "Graphical Representation and Stability Conditions of Predator-Prey Interactions." *The American Naturalist* 97: 209–23.

Spencer, Paul D., and Jeremy S. Collie. 1996. "A simple predator-prey model of exploited marine fish populations incorporating alternative prey." *ICES Journal of Marine Science* 53 (3): 615–28. https://doi.org/10.1006/jmsc.1996.0082.

Stiling, Peter, and Tatiana Cornelissen. 2005. "What makes a successful biocontrol agent? A meta-analysis of biological control agent performance." *Biological Control* 34 (3 SPEC. ISS.): 236–46. https://doi.org/10.1016/j.biocontrol.2005.02.017.

Symondson, W O C, K D Sunderland, and M H Greenstone. 2002. "Can Generalist Predators be Effective Biocontrol Agents?" *Annual Review of Entomology* 47: 561–94. https://doi.org/10.1146/annurev.ento.47.091201.145240.

Van Vuren, Dirk H., Thomas G. Moore, and Chuck A. Ingels. 1998. "Prey Selection by Barn Owls Using Artificial Nest Boxes." *California Fish and Game* 84 (3): 127–32.

Figures

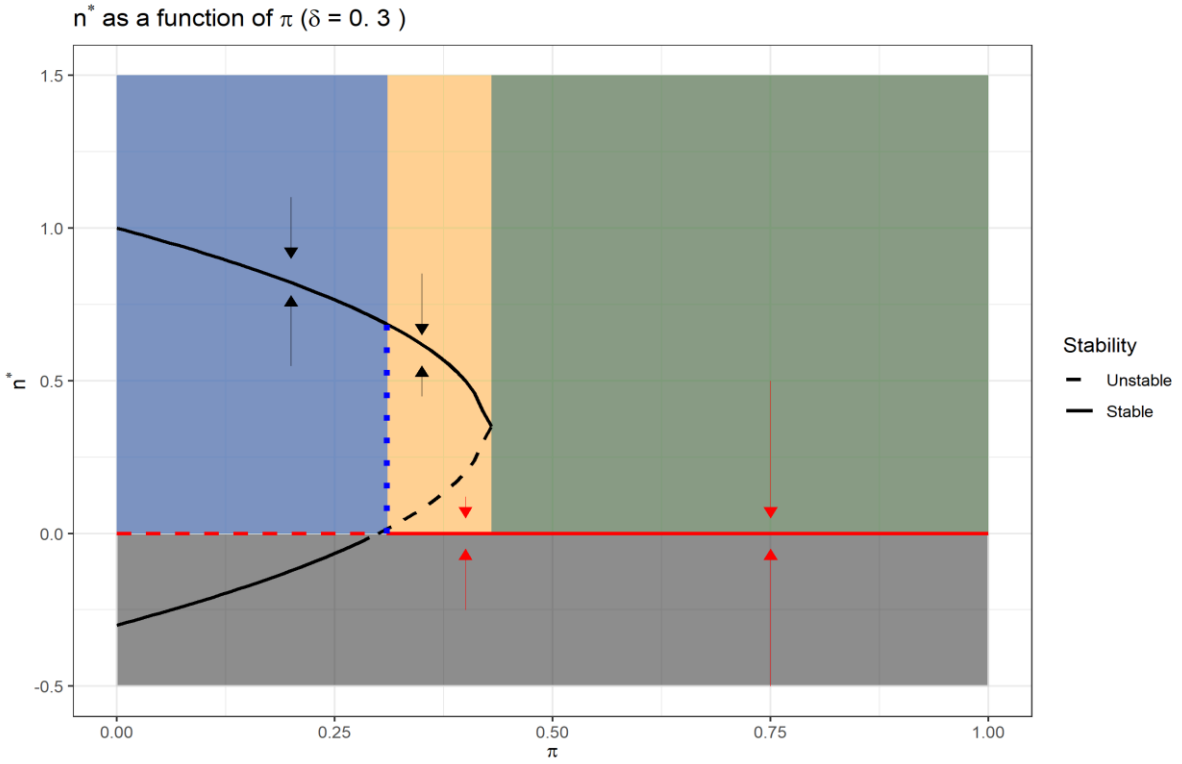

Figure 1: Bifurcation diagram of stability and equilibrium equilibrium prey density as a function of scaled predator density (π) where the scaled half saturation constant is less than 1 ($\delta = 0.3$. There are three qualitative regions: the blue region shows the region where the positive branch of the nontrivial equilibrium is stable and greater than zero, the yellow area represents the area where there is bistability, and the green area represents the area where only the trivial equilibrium is stable and the prey population goes to extinction. The trivial equilibrium is shown in red and switches stability at a transcritical bifurcation where it intersects with the lower branch of the nontrivial equilibrium.

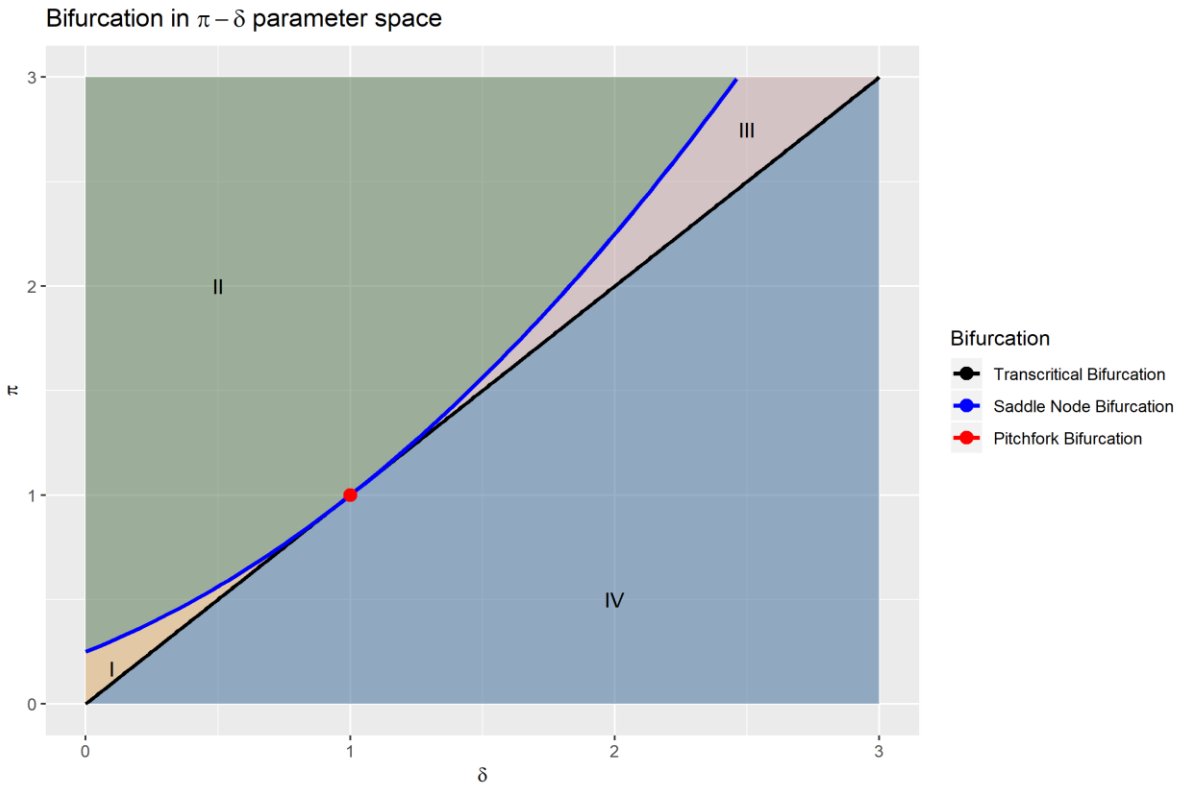

Figure 2: Bifurcation diagram of the equilibrium prey population in the $\pi - \delta$ parameter space for the Type II functional response where π is the scaled predator density and δ is the scaled half saturation constant of the predator. Three types of bifurcations are represented on this plot, the solid black line represents the transcritical bifurcation, the solid blue line is the saddle node bifurcation, and the red dot represents the point in parameter space where the pitchfork bifurcation occurs. The area above the transcritical bifurcation represents where the trivial equilibrium (N_0^*) is unstable, and below it is stable. The area above the blue curve shows where the positive branch of the non-trivial equilibrium (N_+^*) is less than zero, below it, it is greater than zero, meaning that the prey population persists. The yellow shaded area, in a low π and low δ parameter space shows the area of parameters where two stable equilibria exist.

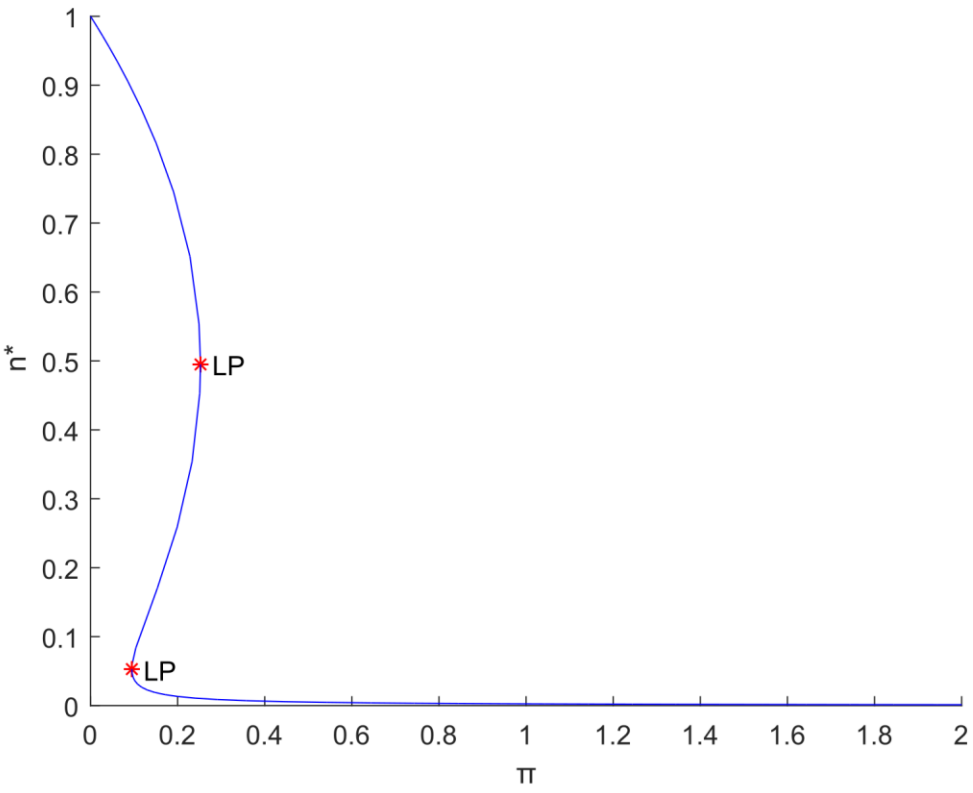

Figure 3: Bifurcation diagram of the equilibrium prey density as a function of scaled predator density where the scaled half saturation constant is less than 1 ($\delta = 0.05$). The two stable, positive equilibria are separated by an unstable equilibrium (the area between the two saddle nodes, labeled here as "LP"). This is analogous to the region of bistability shown in yellow are of Figure 1.

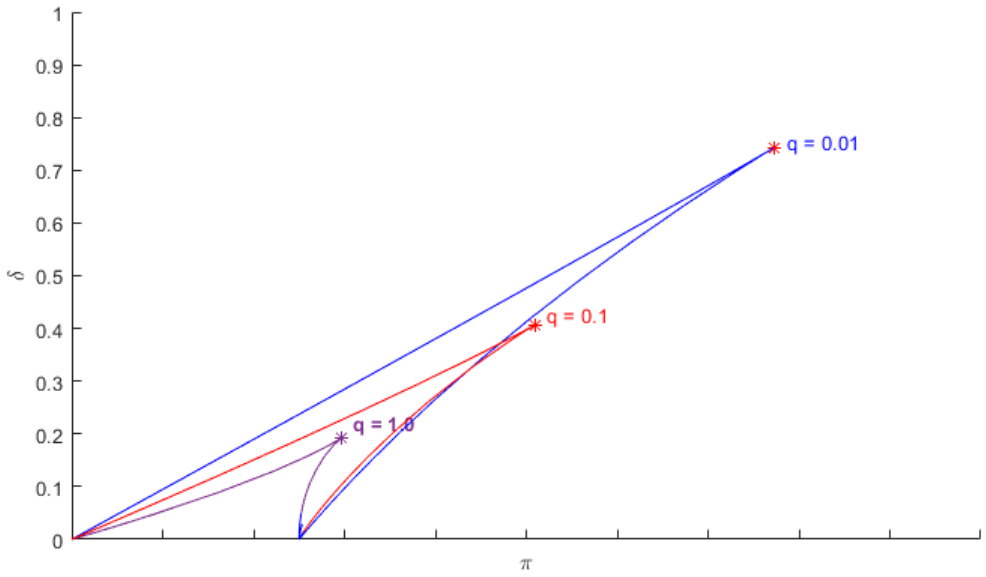

Figure 4: Bifurcation diagram of the equilibrium prey population in the $\delta - \pi$ parameter space for the Type III functional response where π is scaled predator density, δ is the scaled half saturation constant of the predator. Here we show the bifurcation for multiple values of q, including the canonical Type III characterization where $q = 1$ (in red). The area under the triangle represents the area of bistability. Notice that as q increases, the area of bistability decreases.

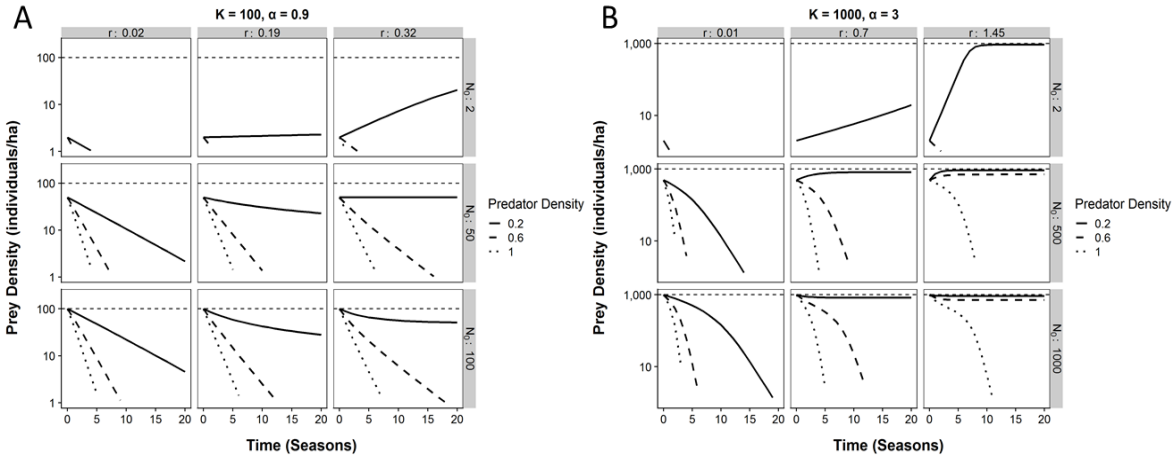

Figure 5: Sample of simulation results for pocket gophers and voles. There are multiple levels of control of prey populations, depending on prey population growth rate, initial density, predator density, carrying capacity, and predator efficiency. Panel A shows different results from simulations of pocket gophers. Panel B shows different results from simulations of voles.

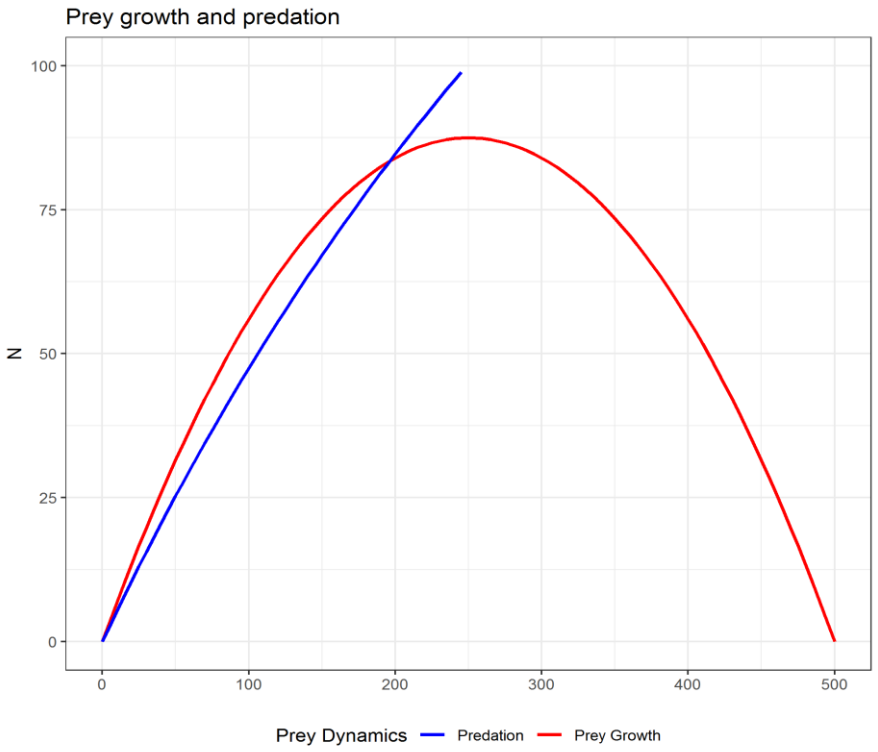

Figure 6: Prey growth and predation for the medium density vole scenario. We can break the Type II prey equation into two parts, the intrinsic growth ($rN(\frac{1-N}{K})$) and the loss due to predation ($\frac{cPN}{N+D}$). Equilibria occur in the places where the two lines intersect. Here we see two intersections (including the intersection at zero), and bistability occurs where the predation curve intersects the intrinsic growth curve at two positive locations. The saddle-node bifurcation occurs for parameters that cause the two curves to be tangent to each other. The overall result is that there is bistability if the predation pressure is strong enough to suppress the prey population

at low density, but not strong enough to overcome the intrinsic population growth when the prey is near $\frac{K}{2}$ (the density that gives maximum total intrinsic population growth).

Tables

Table 1: Predator-prey equation parameter definitions.

Parameter	Definition	Units
P	Predator density	Predators/ha
r	Prey population growth rate	Prey individals/season
K	Carrying capacity of prey	Prey abundance/ha
c	Maximum feeding rate of predators on prey populations	Prey individuals/season
D	Half Saturation constant $\frac{1}{\alpha * h}$	Prey abundance/ha
α	Attack rate or capture efficiency	1/season
h	Handling time $\frac{1}{c}$	Season/prey item

Table 2: Parameter Substitutions for parameter reduction.

Parameter	Definition
n	$\frac{N}{K}$
π	$\frac{cP}{Kr}$
δ	$\frac{D}{K}$
τ	rt

Supplement 1: Bifurcation and Stability Analysis of Non-Numerically Responsive Predator-Prey System with a Type II Functional Response

Predator-Prey Model

Rosenzweig and MacArthur (1963) extended the classic Lotka-Volterra predator prey model with a Type-II functional response (May 1972), which provides a first step to exploring the dynamics between a generalist predator and prey populations. With the Rosenzweig-MacArthur model as a starting point, this study modifies the model to examine the dynamics between a predator whose density does not depend on prey density and a prey population. We use bifurcation analysis to assess the stability and equilibria of prey populations and to determine parameter combinations where stable coexistence exists.

The prey component of the Rosenzweig-MacArthur model is

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{cPN}{N+D} \qquad (1)$$

where the parameters are defined in Table 1 of the manuscript.

Because the predator density does not depend on prey density, the predator density (P) is treated as a parameter instead of a state variable. The parameters can be reduced by simplifying the parameters and substituting, resulting in (See Table 2 of the manuscript for substitutions)

$$\frac{dn}{d\tau} = n(1-n) - \frac{\pi n}{(n+\delta)} \equiv F(n). \qquad (2)$$

Calculating equilibria

To understand the relationship between π and δ we first look at the equilibrium prey population size, where the trivial equilibrium is:

$$n_0^* = 0 \qquad (3)$$

and the nontrivial equilibria are

$$n_+^* = \frac{(1-\delta)+\sqrt{(\delta-1)^2-4(\pi-\delta)}}{2} \quad (4)$$

and

$$n_-^* = \frac{(1-\delta)-\sqrt{(\delta-1)^2-4(\pi-\delta)}}{2}. \quad (5)$$

The trivial equilibrium exists for all values of π and all nonzero values of δ. For certain values of π and δ, the value under the square root in the equations for the nontrivial equilibria will be negative. The resulting complex numbers are not biologically relevant. Therefore, these equilibria only exist if

$$0 \leq (\delta - 1)^2 - 4(\pi - \delta). \quad (6)$$

At the parameter values satisfying the equality, $n_+^* = n_-^* = \frac{(1-\delta)}{2}$. However, one or both of the n^* may be negative, making these mathematical objects biologically irrelevant. n_+^* is positive if $\delta < 1$ or $\delta > 1$ and $\delta > \pi$. n_-^* is positive if $\delta < 1$ and $\delta < \pi$. Figure 1 shows these four regions in $\pi - \delta$ parameter space.

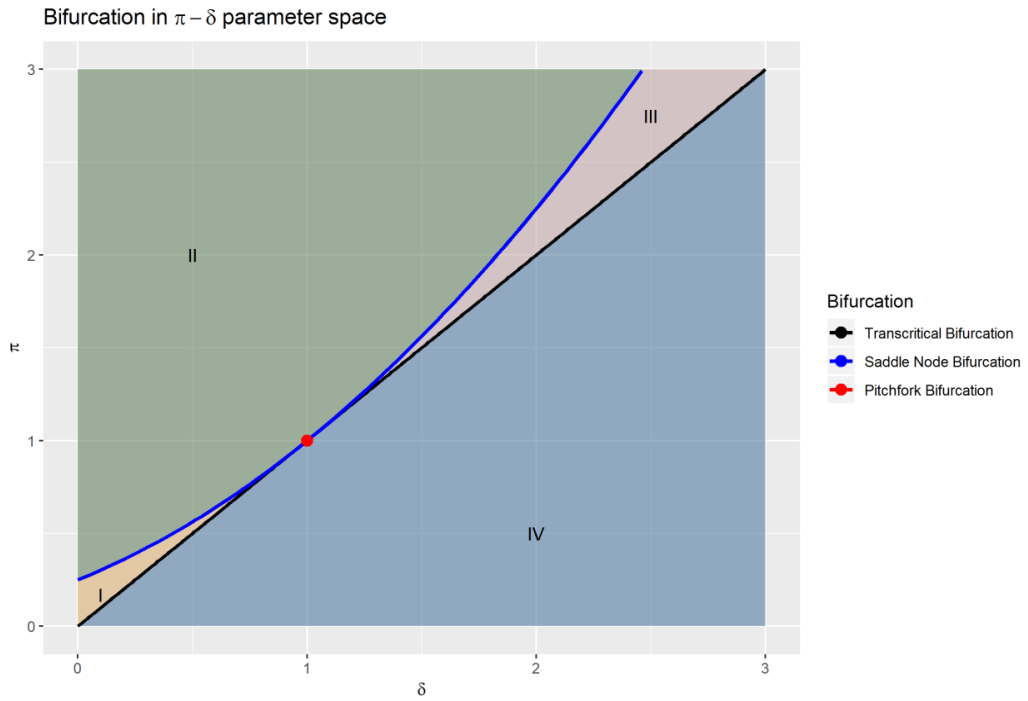

Figure 1: Qualitative patterns of the nontrivial eauilibria, n_+^* *and* n_-^**, across the* π–δ *parameter space: (I) both equilibria are positive; (II) nontrivial equilibria don't exist; (III) both equilibria are negative; (IV)* n_+^* *is positive and* n_-^* *is negative. The bifurcations are described in the text.*

Calculating stability of equilibria

Because this system has a single state variable, we can assess stability by calculating the derivative of the right hand side of equation (7) with respect to n,

$$\mu(n) = \frac{dF}{dn} = 1 - 2n - \frac{\pi\delta}{(n+\delta)^2} \qquad (7)$$

and evaluating it at n^*. If $\mu(n^*) > 0$, then n^* is unstable; if $\mu(n^*) < 0$, then n^* is stable.

For the trivial equilibrium, $\mu(0) = 1 - \frac{\pi}{\delta}$, so n_0^* is stable if $\pi > \delta$ and unstable otherwise (Figure 2).

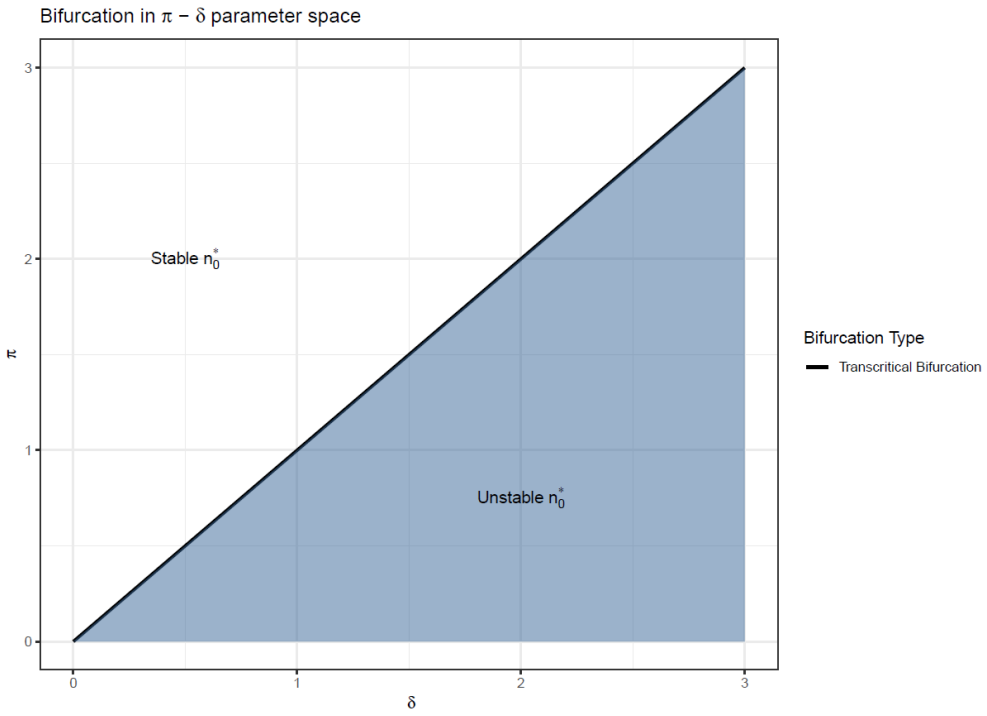

Figure 2: When $\pi > \delta$, n_0^* is stable, and a transcritical bifurcation occurs where $\pi = \delta$. When $\pi < \delta$, n_0^* is unstable (in blue).

Along the curve where the nontrivial equilibria come into existence,

$$\pi = \frac{1}{4}(\delta - 1)^2 + \delta, \quad (8)$$

the equilibrium values are

$$n_+^* = n_-^* \equiv n_\pm^* = \frac{1-\delta}{2}. (9)$$

With the constraint on π, tedious algebra reveals that $\mu(n_\pm^*) = 0$: the pair of nontrivial equilibria are neutrally stable where they appear.

Substituting the general equations for n_+^* and n_-^* into the equation for μ does not give easily interpretable results. However, note that when $\pi = \delta$, $n_+^* = \frac{(1-\delta+|1-\delta|)}{2}$, which is zero if $\delta > 1$, and $n_-^* = \frac{(1-\delta-|1-\delta|)}{2}$, which is zero if $\delta < 1$. Since $\mu(0) = 0$ when $\pi = \delta$, n_+^* undergoes a change of stability at $\pi = \delta > 1$ and n_-^* undergoes a change of stability at $\pi = \delta < 1$.

At $\pi = \delta$, either $n_+^* = n_0^* = 0$ or $n_-^* = n_0^* = 0$. Furthermore, n_+^* or n_-^* passes through zero (rather than being tangent to it) as δ and π are varied in any direction except along the line $\delta = \pi$, and both n_0^* and the crossing nontrivial equilibrium have a change of stability at $\delta = \pi$ (Figure 3 & Figure 4). Thus, this represents a transcritical bifurcation, with n_0^* gaining or losing stability by colliding with n_+^* or n_-^*.

At $\pi = \delta = 1$, $n_\pm^* = 0$ where it appears, creating a pitchfork bifurcation (Figure 5). These bifurcation curves divide the π–δ parameter space into four regions of qualitatively different dynamics, labeled I-IV in Figure 1. Notice that the saddle node bifurcation is tangent to the transcritical bifurcation at $\delta = \pi = 1$, creating the pitchfork bifurcation.

Bifurcations

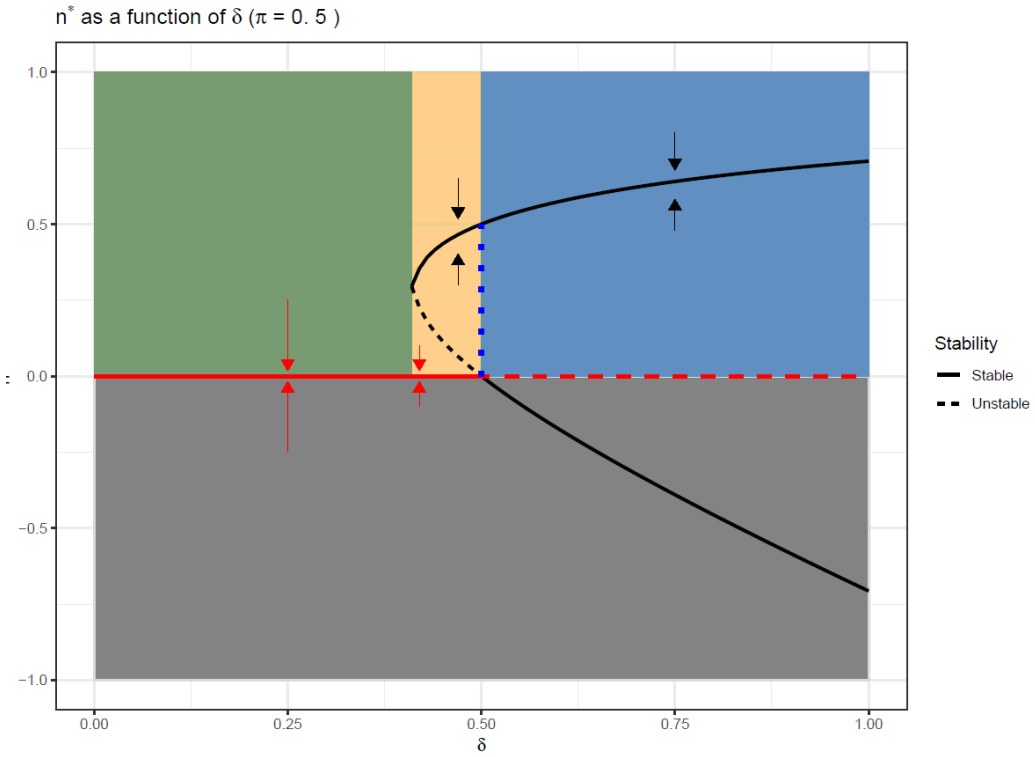

Figure 3: Stability of the trivial (red) and nontrivial (black) equilibria as a function of δ where $\pi = 0.5$. The shaded blocks denote the area of parameter space in the π–δ plot (Figure), where the green area represents Area II where only the trivial equilibrium is stable, the yellow area represents Area I where there is bistability, and the blue represents Area IV where only the positive branch of the nontrivial equilibrium is stable.

We can examine the bifurcations and equilibria by taking horizontal or vertical slices across the δ or π axes to better understand the dynamics. A sample bifurcation diagram, varying δ while keeping π fixed at 0.5, reveals that the appearance of $n_{\pm}^{*}$ at $0 = (\delta - 1)^2 - 4(\pi - \delta)$ is a saddle-node bifurcation (also known as a fold bifurcation or tangent bifurcation), with one branch being stable and the other unstable (Figure 3). There are two stable equilibria at $0.4 < \delta < 0.5$, one at the trivial equilibrium n_0^* and one at the positive branch of the non-trivial equilibrium. At scaled half saturation constants less than 0.4, only the trivial equilibrium is stable, leading to extinction of the prey species. At scaled half saturation constants greater than 0.5, the only stable equilibrium of biological relevance is the positive non-trivial equilibrium. The lower branch of the saddle node bifurcation crosses the trivial equilibrium at $\delta = 0.5$, the transcritical bifurcation, and exchanges stability with the trivial equilibrium. Note, the negative branch of the non-trivial saddle node is stable only in negative state space ($n < 0$) and is therefore biologically irrelevant.

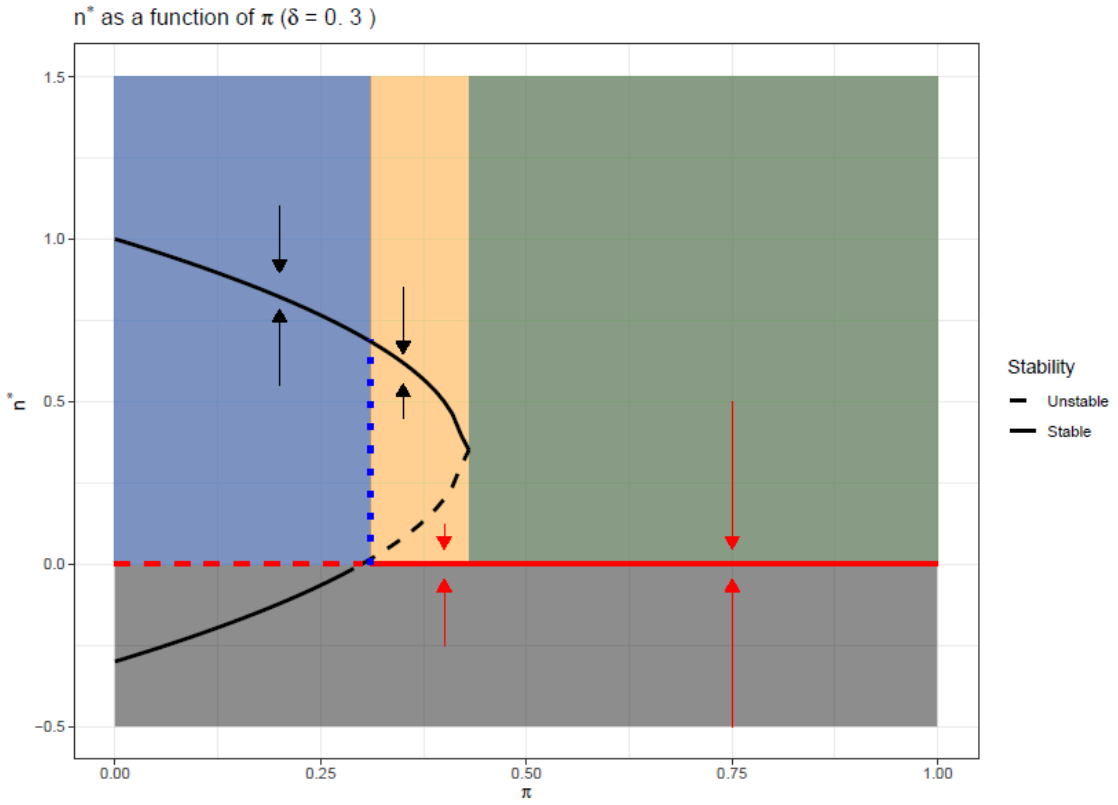

Figure 4: Stability of the trivial (red) and nontrivial (black) equilibria as a function of π *where* $\delta = 0.3$. *The shaded blocks denote the area of parameter space in the* π–δ *plot (Figure), where the blue area represents Area IV where the positive branch of the nontrivial equilibrium is stable and greater than zero, the yellow area represents Area I where there is bistability, and the green area represents Area II where only the trivial equilibrium is stable.*

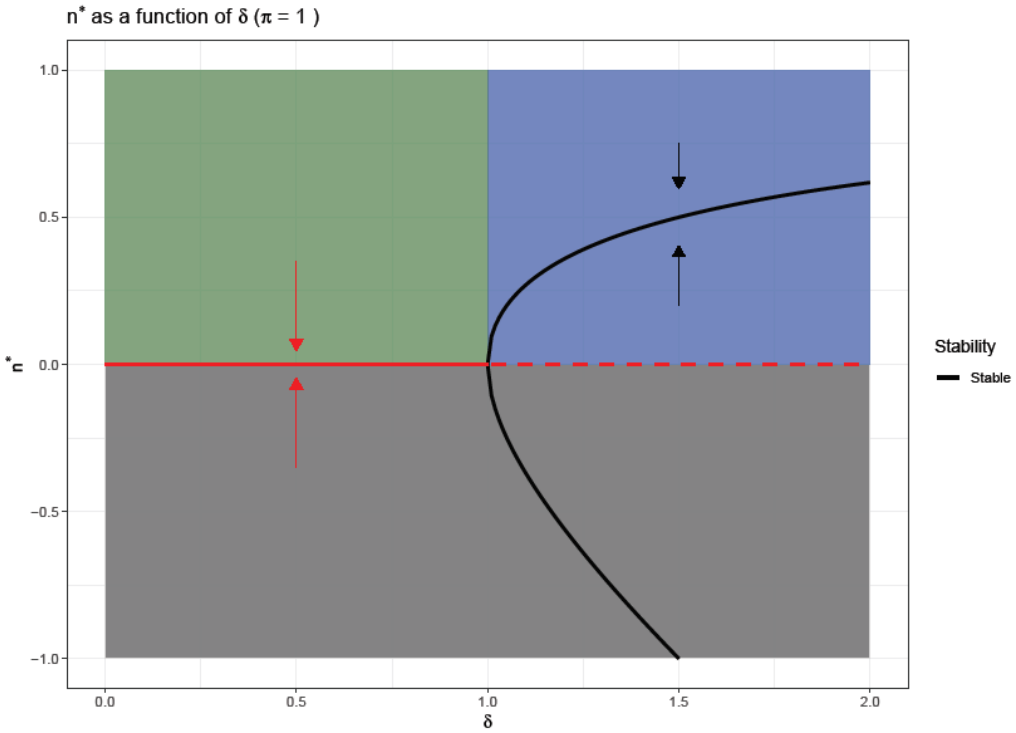

Figure 5: Stability of the trivial (red) and nontrivial (black) equilibria as a function of δ *where* $\pi = 1$*. This plot shows the pitchfork bifurcation where the trivial equilibrium becomes unstable and both branches of the nontrivial equilibrium become stable. In Figure , this bifurcation is denoted as a red point. The green area represents Area II where only the trivial equilibrium is stable and the blue area represents Area IV where the positive branch of the nontrivial equilibrium is stable and greater than zero.*

A similar pattern is seen (albeit in the opposite direction) when varying π while keeping δ fixed (Figure 4). For lower π values, the stable branch of the saddle node shows that the only stable biologically relevant equilibria is the positive, nonzero branch - meaning that the prey population persists at low predator densities. For predator densities between 0.31 and 0.43 (the yellow area inside the curve to the right of the blue dotted line), there are two stable equilibria. For prey populations that are above the unstable, negative branch of the saddle node, the prey population is stable and persists. For populations below the unstable negative branch of the saddle node, n_0^* is stable and the prey population goes extinct. For predator densities above 0.4, the only stable prey density is the trivial equilibrium. The gray shaded area denotes the biologically irrelevant state space.

Figure 5 shows when $\pi = 1$, a pitchfork bifurcation appears at $\pi = \delta = 1$ and both branches of the nontrivial equilibrium are equal to zero. For $\delta < 1$, n_0^* is globally stable; for $\delta > 1$, n_+^* attracts from all positive intitial conditions.

Figure 6 shows the case when π is high ($\pi = 2$). When $\delta < \pi$ the trivial equilibrium is stable, so the prey population goes toward extinction. When $\delta = \pi$, a transcritical bifurcation occurs and the positive branch of the saddle node equilibrium exchanges stability with the trivial equilibrium and the prey population is greater than zero. Note, the negative branch of the non-trivial saddle node is stable only in negative state space ($n < 0$) and is therefore biologically irrelevant.

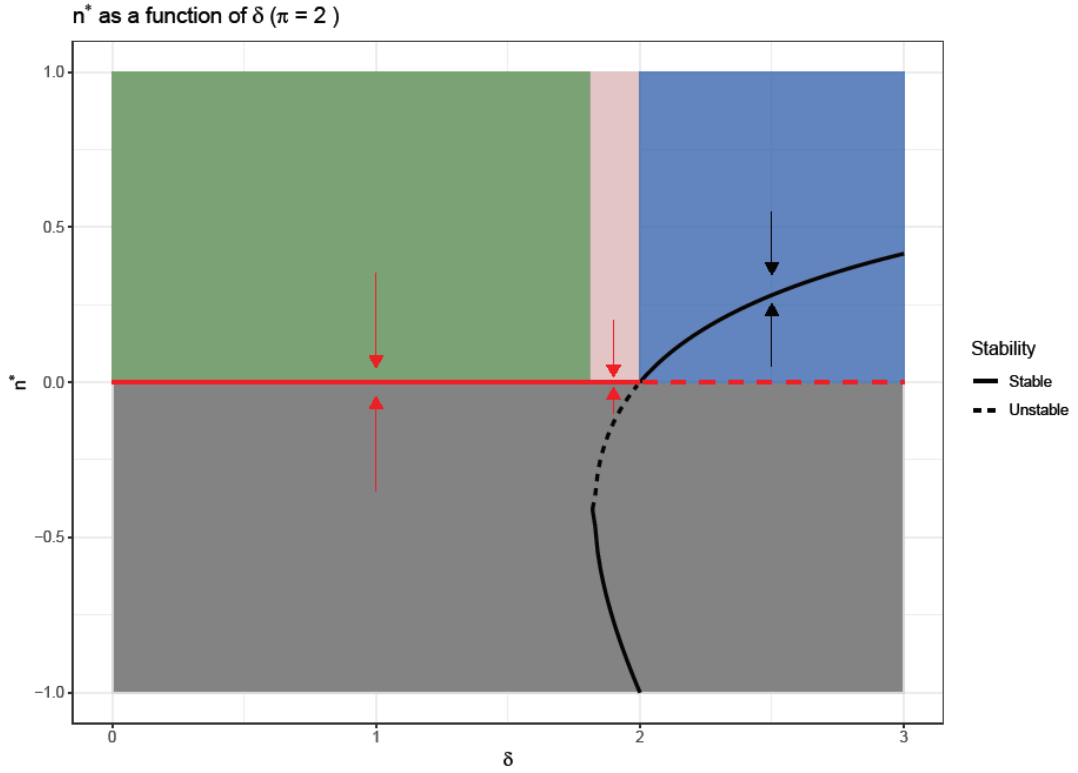

Figure 6: Stability of the trivial (red) and nontrivial (black) equilibria as a function of δ where $\pi = 2$. The shaded blocks denote the area of parameter space in the π–δ plot (Figure), where the green area represents Area II where only the trivial equilibrium is stable, the pink area represents Area III where there is bistability between the trivial equilibrium and the lower branch of the nontrivial equilibrium (though this occurs in negative parameter space) so there is extinction of the prey population, the blue area represents Area IV where the positive branch of the nontrivial equilibrium is stable and greater than zero.

Figure 7 shows the case when δ is fixed at 2. When $\pi < \delta$, the non-trivial, positive branch of the saddle node is the only stable attractor, so the prey population persists. At $\pi = \delta$ a transcritical bifurcation occurs and the non-trivial, positive branch of the saddle node instersects with the trivial equilibrium and exchanges stability. In this area, the lower branch of the nontrivial equilibrium is stable, but occurs in negative parameter space so is biologically irrelevant. When $\pi > \delta$, the trivial equilibrium is stable and the prey population goes extinct. The gray shaded area denotes the biologically irrelevant parameter space.

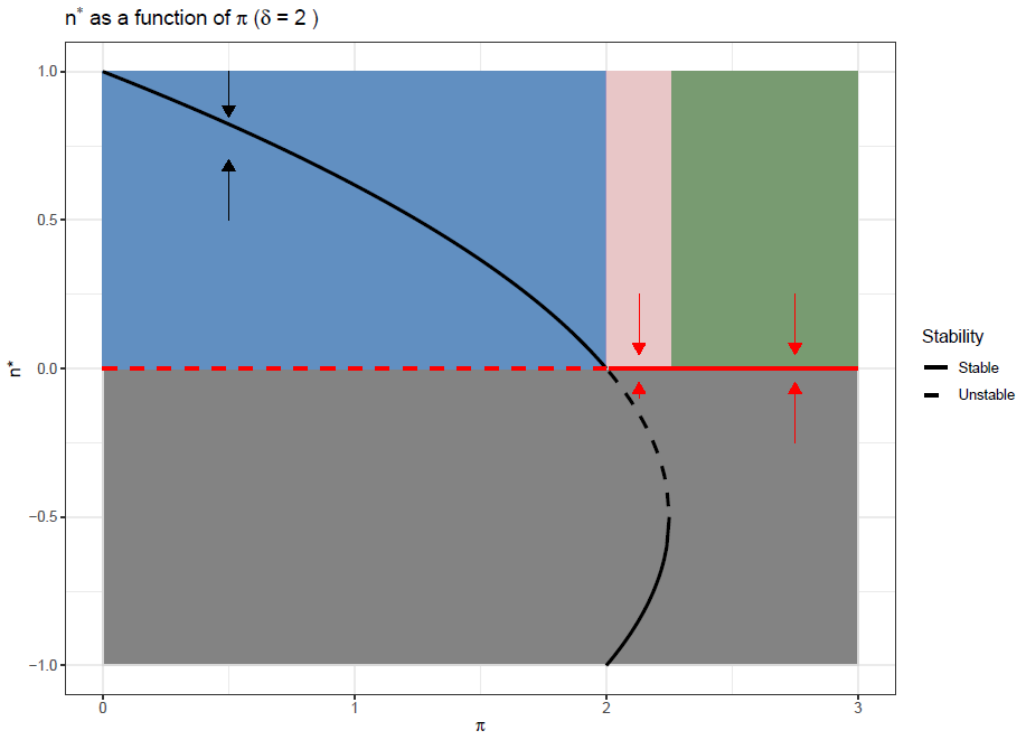

Figure 7: Stability of the trivial (red) and nontrivial (black) equilibria as a function of π *where* $\delta = 2$. *The shaded blocks denote the area of parameter space in the* π–δ *plot (Figure), where the blue area represents Area IV where the positive branch of the nontrivial equilibrium is stable and greater than zero, the pink area represents Area III where there is bistability between the trivial equilibrium and the lower branch of the nontrivial equilibrium (though this occurs in negative parameter space) so there is extinction of the prey population, and the green area represents Area II where only the trivial equilibrium is stable.*

References

May, Robert M. 1972. "Limit cycles in predator-prey communities." *Science* 177 (4052): 900–902. https://doi.org/10.1126/science.177.4052.900.

Rosenzweig, M.L., and R.H. MacArthur. 1963. "Graphical Representation and Stability Conditions of Predator-Prey Interactions." *The American Naturalist* 97: 209–23.

Supplement 2: Bifurcation and Stability Analysis of Non-Numerically Responsive Predator-Prey System with a Type III Functional Response

Predator-Prey Model

Holling (1959) extended the classic Lotka-Volterra predator prey model with a Type III functional response, which explores the dynamics between a predator and prey populations where the predator can switch prey when one prey becomes low in abundance. This formulation of the predator-prey model is sigmoid shaped, and is the typical formulation used for generalist predator interactions with multiple prey species. This study modifies the model to examine the dynamics between a predator whose density does not depend on prey density and a prey population. We use bifurcation analysis to assess the stability and equilibria of prey populations and to determine parameter combinations where stable coexistence exists.

The formulation of the Holling Type III model from Gurney and Nisbet (1998):

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{cN^{q+1}P}{N^{q+1} + D^{q+1}}, \qquad (1)$$

where the parameters are defined in Table 1 of the manuscript.

Because the predator density does not depend on prey density, the predator density is treated as a parameter. The parameters can be reduced by simplifying the parameters and substituting, resulting in (See Table 2 of the manuscript for substitutions)

$$\frac{dn}{d\tau} = n(1-n) - \frac{\pi n^{q+1}}{n^{q+1} + \delta^{q+1}} \equiv F(n). \qquad (3)$$

Notably, the Type III equation includes the parameter q, which is a predator preference for common prey items (Holling 1959). Mathematically, the parameter q A foraging intensity of $q = 1$ is typically used to represent the Type III functional response (Ludwig, Jones, and

Holling 1978), we examine the role of varying q in this supplement, so we do not strictly follow this convention.

Calculating equilibria

To understand the relationship between π and δ we first look at the equilibrium prey population size, where the trivial equilibrium is

$$n_0^* = 0. \qquad (4)$$

And the nontrivial equilibria are the solutions of

$$n^* = (1-n)(n^{q+1} + \delta^{q+1}) - \pi n^q. \qquad (5)$$

We used bifurcation analysis to identify changes in stability of each equilibria or to identify when new equilibria appear. Because this system has a single state variable, we can assess stability by examining the derivative of the function, resulting in

$$\mu = \frac{dF}{dn} = 1 - 2n - \frac{n^q \delta^{q+1} \pi (q+1)}{(n^{q+1} + \delta^{q+1})^2}. \qquad (6)$$

Differentiating with respect to n and evaluating at $n = 0$ reveals that the trivial equilibrium is always unstable if $q > 0$. Yet, when q is close to zero, the dynamics should be similar to the type-II model. The nontrivial equilibrium is

$$n^* = (1-n) - \frac{\pi n^q}{n^{q+1} + \delta^{q+1}} \qquad (7)$$

Unlike the Type II functional response, we cannot solve for this equilibrium numerically, so we used the bifurcation software MatCont (Dhooge, Govaerts, and Kuznetsov 2003), a MatLab GUI extension to assess the stability of the equilibria.

Bifurcations

Similar to what we did with the Type II functional response, we can examine various horizontal and vertical slices across the π-δ parameter space. First, we can examine a fixed $\pi =$

0.5, where we also fix $q = 1$ (Figure S2.1). We find an equilibrium at $\pi = 0.25$. Instead of intersecting the zero equilibrium and creating a transcritical bifurcation like we saw in the Type II, there is a second saddle node bifurcation ($\pi = 0.09$), and for values of π to the right of that bifurcation there is a stable equilibrium that's just a little bit larger than zero. For values of π between the two saddle bifurcations, there are two stable equilibria, just like there are for the type II model between the transcritical bifurcation and saddle node bifurcations.

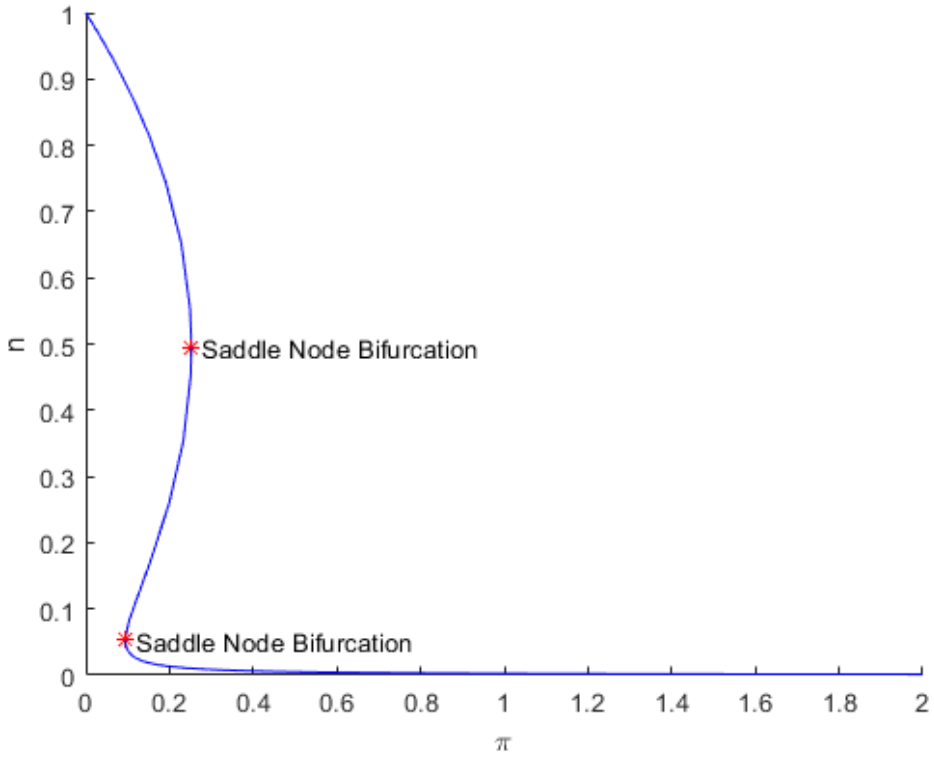

Figure S2.1: Bifurcation diagram when δ is fixed at a low value ($\delta = 0.05$). The area between the two saddle node bifurcations is unstable, whereas the area above and below are stable. The trivial equilibrium is always unstable.

We can examine this relationship for a fixed higher value of $\delta = 0.5$. When $\delta > \pi$, the equilibrium is always stable (Figure S2.2). The prey population persists.

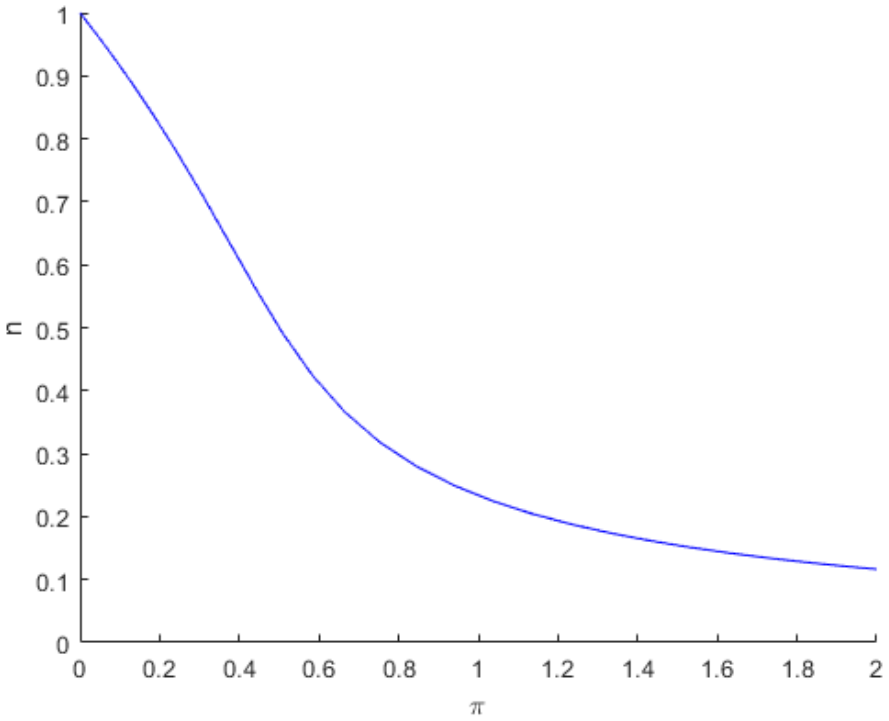

Figure S2.2: Bifurcation diagram when $\delta = 0.5$. Notice that the saddle nodes disappear and the nontrivial equilibrium is stable. The trivial equilibrium is always unstable.

Looking at this relationship in $\delta - \pi$ parameter space, we see a cusp bifurcation. The cusp is where the two limit points intersect; between the two curves is the area of bistability. Below the region of bistability, the only stable equilibrium is "large;" above it (large π) it is close to zero (Figure S2.3). To the right of the cusp, there is no bistability, but the one equilibrium transitions continuously from large to small as π increases. Close to the cusp, that transition can be quite steep; here it is for $\delta = 0.05$:

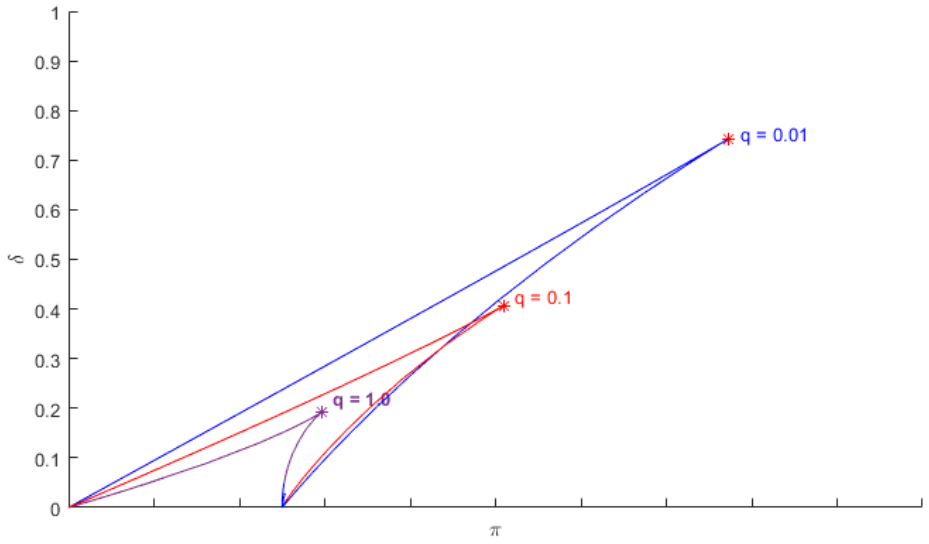

Figure S2.3: Relationship between δ and π. The area between the two curves is the area of bistability where there is a stable equilibrium at a higher n and an n* close to zero. As q increases, the area of bistability decreases.*

Notice that here, where $q = 0.01$, the cusp has moved away from (1,1) (the value for the type-II model). We also see that the area of bistability decreases as q increases (Figure S2.3).

References

Dhooge, A., W. Govaerts, and Yu A. Kuznetsov. 2003. "MATCONT: A MATLAB package for numerical bifurcation analysis of ODEs." *ACM Transactions on Mathematical Software* 29 (2): 141–64. https://doi.org/10.1145/779359.779362.

Gurney, W.S.C., and R.M. Nisbet. 1998. *Ecological Dynamics*. 1st ed. New York, NY: Oxford University Press.

Holling, C.S. 1959. "The Components of Predation as Revealed by a Study of Small Mammal Predation of the European Pine Sawfly." *The Canadian Entomologist* XCI (5): 234–61.

Ludwig, D., D.D. Jones, and C.S. Holling. 1978. "Qualitative Analysis of Insect Outbreak Systems : The Spruce Budworm and Forest." *Journal of Animal Ecology* 47 (1): 315–32.

Supplement 3: Simulation of Pocket Gopher and Vole Population Responses to Generalist Predators

Pocket gophers (*Thomomys* spp.) and voles (*Microtus* spp.) cause significant damage to numerous agricultural crops in the American West (e.g. gophers: Askham (1988); Baldwin et al. (2014); Howard and Childs (1959); Luce, Case, and Stubbendieck (1981); Marsh (1994); Miller (1953); Smallwood and Geng (1997), voles: Askham (1988), Baldwin et al. (2014); Witmer et al. (2009)). Because pocket gophers are a fossorial rodent that consume both aboveground and belowground portions of plants, their populations are highly responsive to vegetation cover and soil types (Sullivan and Hogue 1987). Pocket gopher burrows can threaten earthen levee systems (Ordeñana, Van Vuren, and Draper 2012), spread weeds (Cook 1939), and damage subsurface drip irrigation systems (Montazar et al. 2017). Voles forage on both the underground and aboveground biomass of plants, and can kill woody plants by girdling their trunks, or cause sub-lethal damage leading to reduced growth and yields (Byers 1984; Clark 1984; Merwin, Ray, and Curtis 1999). Vole populations commonly undergo eruptive fluctuations every few years as a result of food availability, environmental stochasticity, and possibly predator densities (Batzli and Pitelka 1971; Beacham 1979a; Boonstra 1977; Chitty and Phipps 1966; Cockburn and Lidicker 1983; Korpimäki and Krebs 1996; Krebs 1966; Murray 1965). While both pocket gophers and voles cause significant damage in agricultural fields, pocket gophers are considered ecosystem engineers in natural systems, where their burrowing and foraging activity can change soil structure, alter aboveground biomass, and prevent tree establishment and succession in grasslands (Cantor and Whitham 1989; Jenkins and Bollinger 1989; Miller 1957; Reichman and Smith 1985). Pocket gophers and voles are also an important component of natural food webs, and vacated pocket gopher burrows are used by several species of conservation concern (Smallwood, Geng, and Zhang 2001).

We simulated the population dynamics of two common rodent pests of farms in Western North America, the pocket gopher and the vole in the presence of a generalist predator. Using available data from agricultural settings, we varied predator density (representing different levels of control), prey growth rate, carrying capacity, and predator attack rate (accounting for uncertainties in these biological parameters). For each parameter scenario we simulated the rodent populations over a five year time horizon to represent a management relevant time scale.

Parameter Calculations

Calculating prey growth rates (r)

We created stage-structured population matrices for both pocket gophers and voles using data extracted from the literature. Stage-structured population matrices can be used to calculate population growth rates for species based on multiple, distinct age-based stages. These stages account for the probability that an individual within a given stage will survive or move into the next stage, and whether each individual will produce offspring within a given time step. Individual animals 'enter' a given stage at the start of a time step and by the next time step they will either move into the next stage, remain within the same stage, or die. Individuals may also reproduce within the time step, and new offspring are added to the lowest stage structure (Figures 1 - 3). Our predator-prey models utilized 3-month long seasonal time steps and all demographic data were scaled to the same seasonal timing.

For both pocket gophers and voles, the instantaneous rate of population growth (r) was calculated by first calculating the geometric population growth rate (λ) from the stage structured matrices using the popbio package in R (Stubben and Milligan 2007). The popbio package calculates λ by identifying the dominant eigenvalue in a population matrix. From λ, we can calculate the parameter r, using the approximation $r = log_e \lambda$. This conversion allows us to

move from a structured (matrix) to an unstructured (logistic growth) model, but it requires the assumption that there are no time lags associated with growth and that the matrices are derived from measurements taken when the population is not experiencing density dependence. Thus, the estimates of r should be viewed as rough approximations of possible growth rates for what both pocket gopher and vole populations might be.

We used female vole and pocket gopher data from the literature to construct population matrices (Tables 1 - 3). Populations were modelled using a seasonal time step (~13 weeks), which suggests that the population will be reproducing each season. This was used to represent a continuously reproducing population and to capture the fact that rodent populations can reproduce throughout the year. For both vole and gopher populations, if the minimum calculated growth rate was negative, a minimum r of 0.01 was chosen to represent very low (but still positive) growth in the vole and pocket gopher populations. Because this analysis is particularly interested in pests which have a positive growth rate, we wanted to ensure that positive growth was reflected. All matrices were constructed to represent a post-breeding census.

Pocket Gopher Population Growth Rates

For pocket gophers, the appropriate stage-structure classifications are based on maternal care, pelage, and reproductive status. Juvenile pocket gophers are still under maternal care and do not leave their maternal burrow system where they remain for 35-45 days prior to weaning (Howard and Childs 1959), sub-adult pocket gophers have left their maternal burrow systems but are smaller than fully-grown adult females and have a pubic symphysis gap of <6mm so have not yet reproduced, and adult pocket gophers are sexually mature and have a fully dissolved pubic symphysis gap >6mm (Loeb 1990). There are no data in the literature on the survival rates of juvenile pocket gophers, most likely because juveniles do not leave their maternal burrows and are therefore rarely caught during field studies. Therefore, we have used a value of 0.5,

which is the same as vole survival in the juvenile stage. The length of time that pocket gophers spend in sub-adult stages prior to breeding depends on when they are born, with individuals born early in the spring potentially breeding in their first year, and those born in summer or fall generally waiting until the following spring to breed, although breeding can occur year-round in some areas and habitats (e.g. Miller (1946); Loeb (1990)), but generally is once females are 7 months old (Daly and Patton 1986).

Because age at maturity is variable across pocket gopher populations, we examined the role of two different life histories on population growth rates – the first where individuals become sexually mature after six months (Table #label(tab:tab1), Figure 1) and the second where individuals become sexually mature after nine months (Table #label(tab:tab2), Figure 2). The minimum, mean, and maximum growth rates used in the simulations is reflected by the minimum, mean, and maximum of the aggregated matrices in both the six and nine-month scenarios.

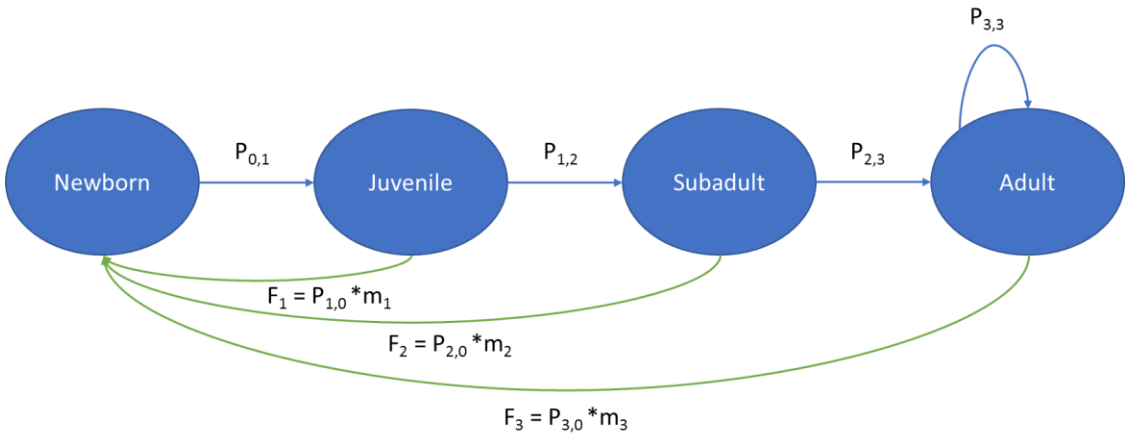

Figure 1: Gopher life cycle diagram with maturity at six months. $P_{0,1}$ *is the probability a newborn will survive and become a juvenile.* $P_{1,2}$ *is the probability a juvenile will survive and become a sub-adult.* $P_{2,3}$ *is the probability a sub-adult will survive and become and adult.* $P_{3,3}$ *is the probability and adult will survive and remain an adult.* F_1 *is the fecundity of juveniles* ($m_1 P_{0,1}$). F_2 *is the fecundity of subadults* ($m_2 P_{1,2}$). F_3 *is the fecundity of adults* ($m_3 P_{2,3}$).

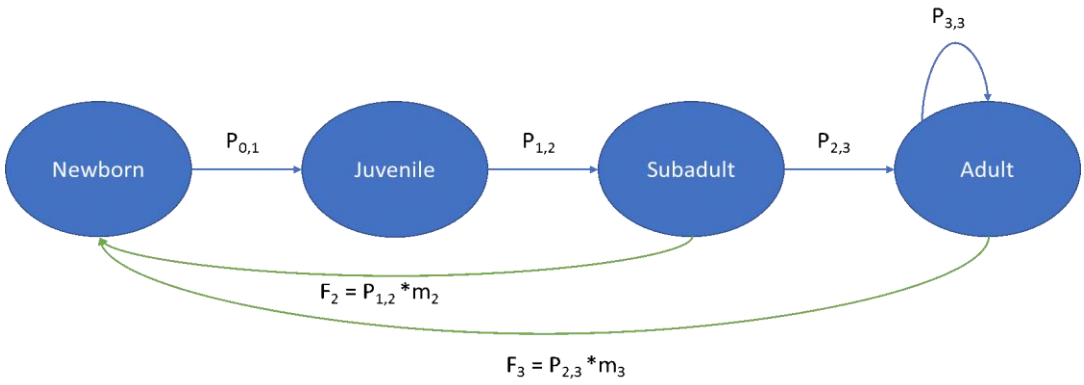

Figure 2: Gopher life cycle diagram with maturity at nine months. $P_{0,1}$ *is the probability a newborn will survive and become a juvenile.* $P_{1,2}$ *is the probability a juvenile will survive and become a sub-adult.*$P_{2,3}$ *is the probability a sub-adult will survive and become an adult.* $P_{3,3}$ *is the probability an adult will survive and remain an adult.* F_2 *is the fecundity of sub-adults (*$m_2 P_{1,2}$*).* F_3 *is the fecundity of adults (*$m_3 P_{2,3}$*).*

Vole Population Growth Rates

Vole demographic data were extracted in the same way as pocket gophers, but it is important to note that survival measurements include some from *M. townsendii* in addition to measurements from *M. californicus* to include more studies from agricultural habitats. Because this study was exploratory in nature, this provides a good first approximation for how we might expect vole populations to grow over time. For voles, stage is classified based on age and pelage. Voles are classified as juvenile from birth to approximately 3 weeks of age, sub-adult from 3 weeks to 8-9 weeks, and adults thereafter (Cudworth and Koprowski 2010). Because of the rapid transition from juvenile to subadult, only two stages were represented in the matrix models – juvenile and adult, with juveniles reproducing at the end of their stage transition (Table #label(tab:tab3), Figure 3). Given the unique life cycle of vole populations, r was calculated using a 10-week time step in the matrix models, approximating five generations per year. r was then adjusted to reflect a seasonal growth rate (approximately 13 weeks) for consistency of a seasonal time step in the predator-prey models.

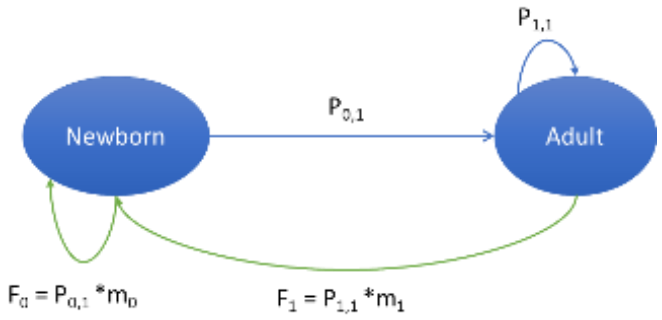

Figure 3: Vole life cycle diagram. $P_{0,1}$ *is the probability a newborn will survive and become a juvenile.* $P_{1,1}$ *is the probability an adult will survive and remain an adult.* F_0 *is the fecundity of the newborn class (*$m_0 P_{0,1}$*).* F_1 *is the fecundity of adults (*$m_1 P_{1,1}$*).*

Calculating the maximum predator feeding rate (k_{max}*)*

Kross and Baldwin (2016) assembled information on diets and energetic needs of barn owls to estimate the total number of rodents needed to supply a barn owl nest box over the course of a year. That analysis assumed a mixed diet of gophers, voles and mice. We used the values in their Table 1 to calculate the number of gophers consumed by barn owls to supply these needs in a gopher-only diet, and the number of voles consumed by barn owls to supply these needs in a vole-only diet.

Simulation Results

Simulations were run over a period of 20 seasonal (~13-week) time steps for pocket gophers and voles (5 years total), with all analyses conducted in R v. 3.5.0 (R Development Core Team 2018). Simulations were run for these relatively short periods of time to focus on outcomes in a management-relevant time scale. Tables #label(tab:tab4) and #label(tab:tab5) shows the range or N_0, P, α, r, and K_{prey} values used in simulations; for reference, the tables also include calculated annual prey growth rates.

Pocket Gopher simulations

Under all scenarios, the presence of barn owls resulted in pocket gopher populations remaining below the environmental carrying capacity at the end of 5 years (Figures 4 - 6). In scenarios where initial pocket gopher populations were intermediate (approximately $0.5K_{prey}$), barn owl predation led to a reduction in gopher population densities under all scenarios except at the lowest barn owl densities. For example, with a carrying capacity of 100 individuals/ha and a moderate owl attack rate (α), there were varying degrees of control depending on the growth rate and initial size of the gopher population (Figure 5). For moderate to high gopher growth rates, and with a very low owl density there was some persistence of pocket gopher populations, but they remained below K_{prey}. Under the lowest predator attack rate, the gopher population was never driven to extinction, no matter how low the population growth rate was. In contrast, at the highest owl attack rate the gopher populations were driven to extinction in 100% of the scenarios.

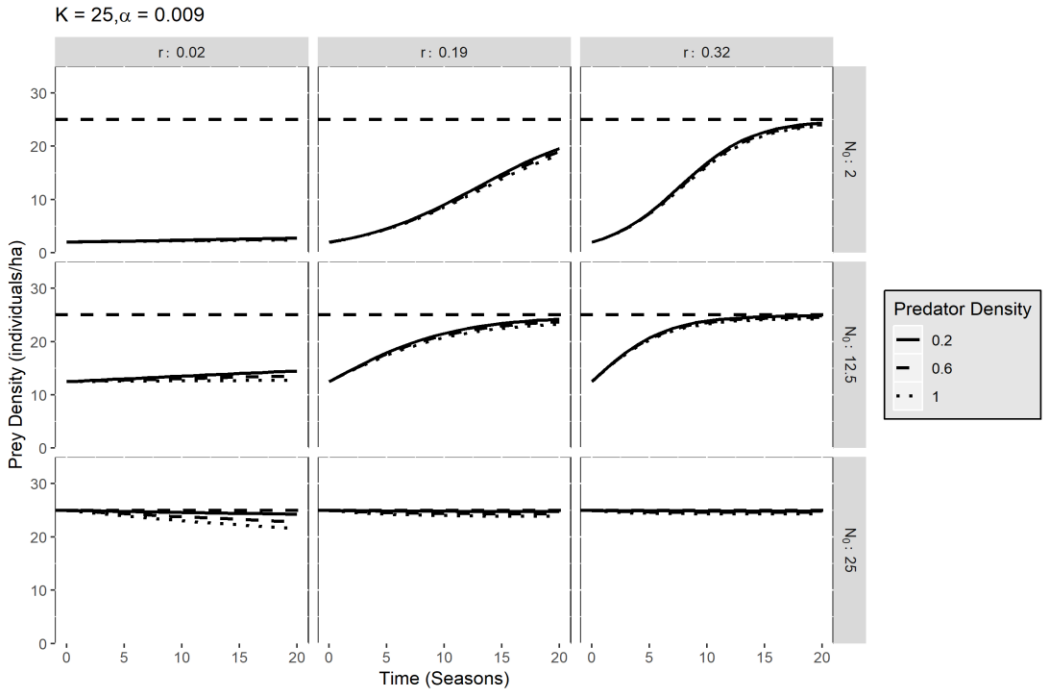

Figure 4: Gopher simulations over a five year period with low carrying capacity ($K_{prey} = 25$) and low predator attack rate ($\alpha = 0.009$). The rows represent different initial prey population densities and the columns represent different prey growth rates. Time (on the x-axis) is represented in three month seasons, for a total of five years and prey density (on the y-axis) is in individuals/ ha.

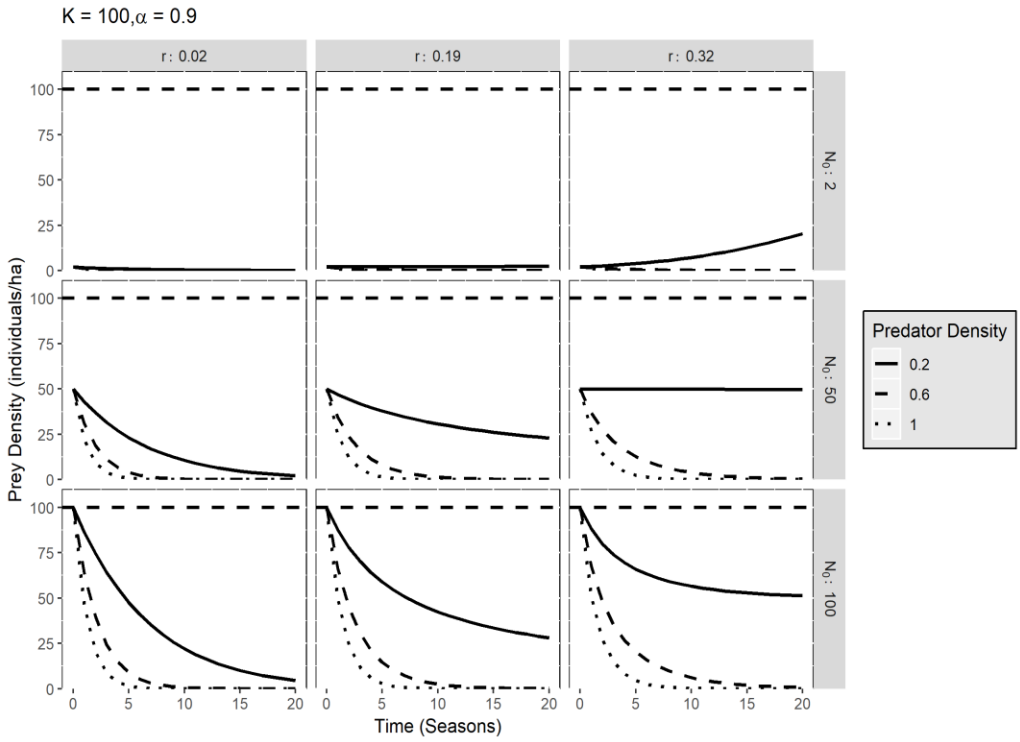

Figure 5: Gopher simulations over a five year period with medium carrying capacity ($K_{prey} = 100$) and medium predator attack rate ($\alpha = 0.9$). The rows represent different initial prey population densities and the columns represent different prey growth rates. Time (on the x-axis) is represented in three month seasons, for a total of five years and prey density (on the y-axis) is in individuals/ha.

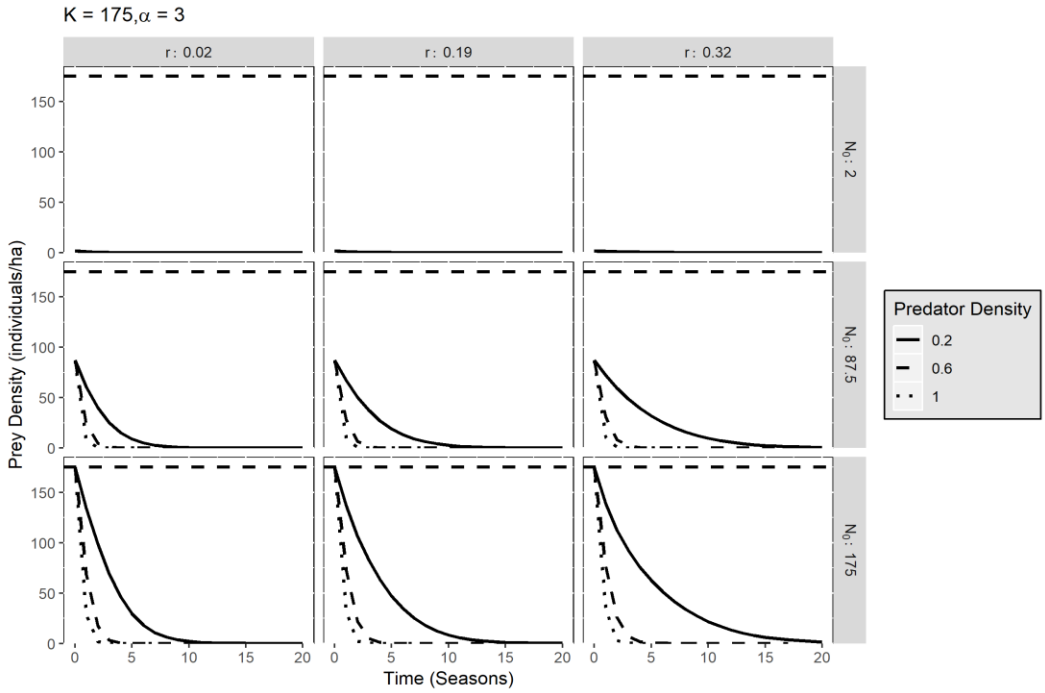

Figure 6: Gopher simulations over a five year period with high carrying capacity ($K_{prey} = 175$) and high predator attack rate ($\alpha = 3$). The rows represent different initial prey population densities and the columns represent different prey growth rates. Time (on the x-axis) is represented in three month seasons, for a total of five years and prey density (on the y-axis) is in individuals/ha.

Vole simulations

Under all simulations, the presence of barn owls resulted in vole populations remaining below the environmental carrying capacity at the end of five years (Figures 7 - 9). Similar to the pocket gopher simulations, there was variability in whether or not vole populations were driven to extinction or coexisted with barn owl populations (Figure 8). Across all attack rates (α), extinction was achieved in all scenarios with the lowest vole population growth rates ($r = 0.01$). Across all α values under medium vole population growth ($r = 0.7$), extinction was achieved in 52% of scenarios (range = 0-820 individuals/ha, mean 87.5 individuals/ha). Under the highest owl density (1.0 active nests/ha), extinction was achieved in all scenarios. At the medium owl densities (0.6 active nest/ha), owls provided some control of rodent populations at all growth

rates, whereas, at the lowest predator density (0.2 active nest/ha), extinction was not observed in scenarios for medium and high vole population growth rates.

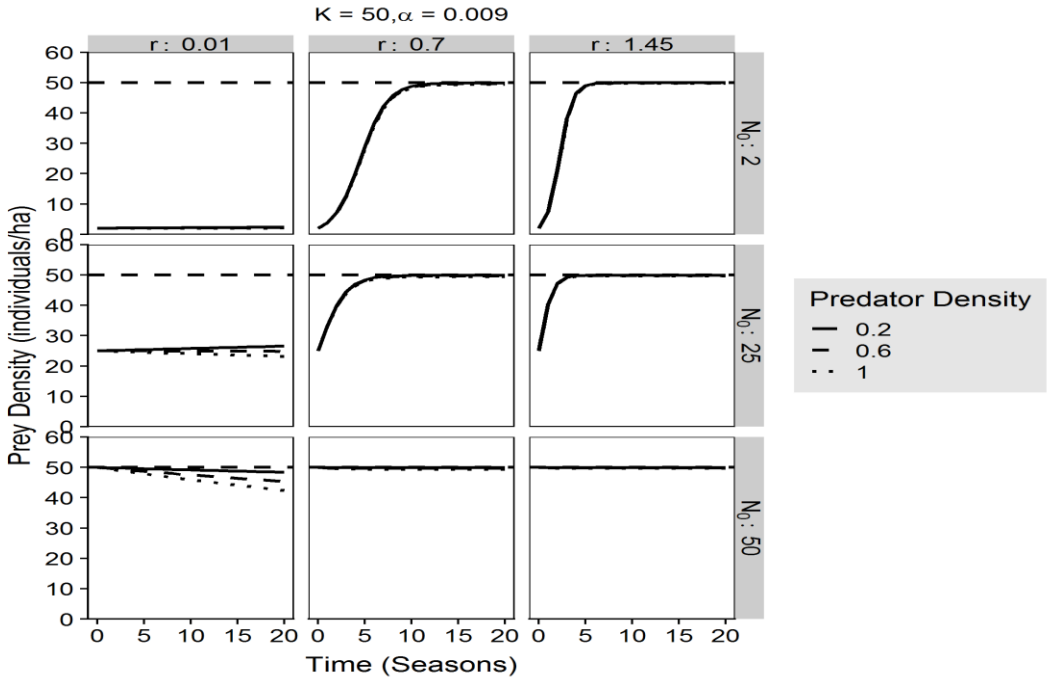

Figure 7: Vole simulations over a five year period with low carrying capacity ($K_{prey} = 50$) and low predator attack rate ($\alpha = 0.009$). The rows represent different initial prey population densities and the columns represent different prey growth rates. Time (on the x-axis) is represented in three month seasons, for a total of five years and prey density (on the y-axis) is in individuals/ha.

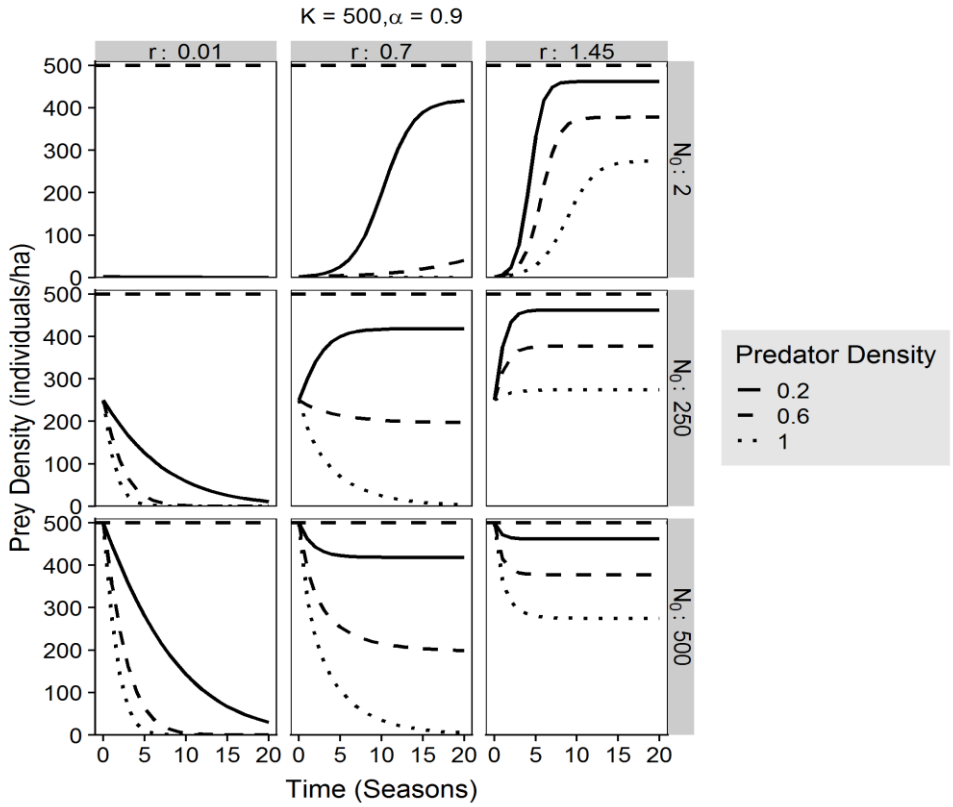

Figure 8: Vole simulations over a five year period with medium carrying capacity ($K_{prey} = 500$) and medium predator attack rate ($\alpha = 0.9$). The rows represent different initial prey population densities and the columns represent different prey growth rates. Time (on the x-axis) is represented in three month seasons, for a total of five years and prey density (on the y-axis) is in individuals/ha.

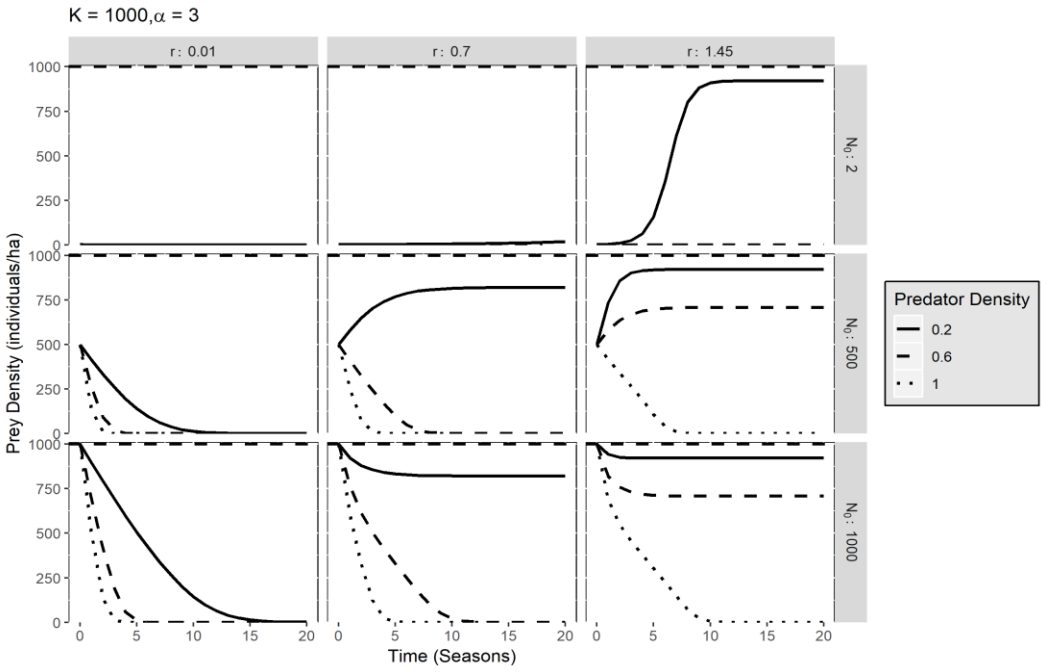

Figure 9: Vole simulations over a five year period with high carrying capacity ($K_{prey} = 1000$) and high predator attack rate ($= 3$). The rows represent different initial prey population densities and the columns represent different prey growth rates. Time (on the x-axis) is represented in three-month seasons, for a total of five years and prey density (on the y-axis) is in individuals/ha.

Discussion

The potential range of rodent population reduction was affected by rodent population growth rates, initial rodent population size, barn owl attack rates, and barn owl population densities, suggesting that barn owl presence could be a useful tool to incorporate into an IPM program. Previous field studies have demonstrated mixed results in the role of raptors as a significant contributing factor in the decline of Microtine populations (Klemola et al. 1997; Korpimäki and Krebs 1996; Labuschagne et al. 2016; Maher 1970; Nie and Liu 2005). Our models suggest that this lack of generality may be partly due to study-to-study heterogeneity in rodent growth rates and predator abundances. For example, where vole populations exhibited low intrinsic growth rates we observed a substantial reduction in vole numbers from barn owl

predation under all predator densities, but under higher vole intrinsic growth rates control required barn owl densities to be high.

As with all population models, our simulation results and subsequent interpretation are limited by various factors. Data on the population dynamics of pocket gophers and voles from agricultural fields in our study area are limited (Kross and Baldwin 2016). The majority of the data published on these key pest species comes from rangelands, orchards, alfalfa fields, and natural grasslands, and shows that populations can vary significantly in reproductive rates, mortality, and territory sizes under different environmental and habitat conditions. Additionally, most of the data extracted for barn owl diets came from vineyards, yet barn owl diet varies significantly across cropping systems (Kross, Bourbour, and Martinico 2016), suggesting that the barn owl and pocket gopher data we used for our models may not completely overlap. Field studies to better understand the effects of barn owls on prey populations under different conditions are essential, especially given the inability of our models to incorporate the many complex factors that affect owls, rodents, and farmer income (Figure 10).

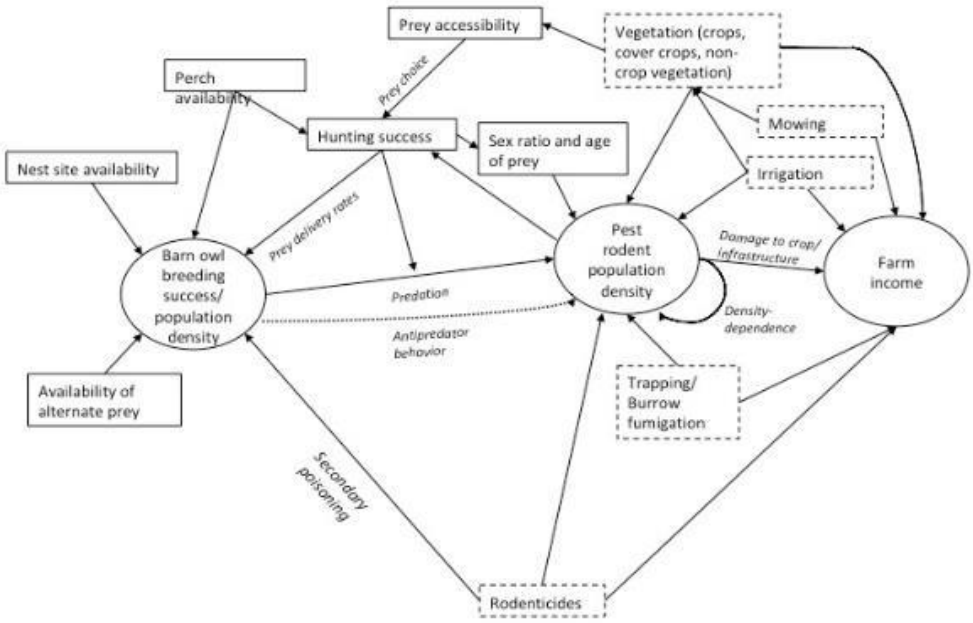

Figure 10: Conceptual model of the factors affecting the efficacy of barn owl control of rodent pests on farms. Boxes with dashed lines indicate farm management practices, arrows represent processes and effects that boxes have on each other. Establishment and cleaning of barn owl nest boxes will also affect farm income.

We built our models using seasonal timesteps to provide results that are on a realistic management timescale for farmers, but we used an annual average for barn owl hunting effort and rodent reproductive output rather than including variation in these variables across seasons. Our models also do not allow for the complex multiannual fluctuations that occur in some Microtine populations (e.g. Krebs (1966)). This is of note given that previous studies have hypothesized that predators are unlikely to play a significant role in limiting population growth of rapidly increasing or peak populations (Beacham 1979b; Boonstra 1977; Korpimäki and Krebs 1996). Furthermore, seasonality in models of specialist predators can result in complex dynamical outcomes (Rinaldi, Muratori, and Kuznetsov 1993). Therefore, we do not expect our models to be precise predictions of field results. Nevertheless, if the parameters are viewed as

annual averages, we expect that our results should provide guidance on long-term trends that would result from owl use as a biocontrol agent.

Tables

Table 3.1: Stage-structured matrices used for pocket gophers reaching sexual maturity at six months, showing probability that an individual within each stage will survive and move to the next stage and the fecundity (number of offspring) that an individual of each stage will produce within a time step. Models based on minimum, mean (between min and max), and maximum values found in the literature are shown side by side. See Figure 1 for the life cycle diagram showing which probabilities are represented in each cell of the tables. ([1]Loeb 1990, [2]Anderson & MacMahon 1981, [3]Daly & Patton 1986, [4]Howard & Childs 1959, [5]Scheffer 1938).

	Newborn	Juvenile	SubAdult	Adult
Minimum				
Newborn	x	$0.6^{1} * 0.50$	$1.69^{1} * 0.66^{2}$	0.75^{3}
Juvenile	0.5	x	0	0
SubAdult	0	0.5	x	0
Adult	0	0	0.66^{2}	0.75^{3}
Mean				
Newborn	x	$0.63^{1} * 0.50$	$2.97^{1,4,5} * 0.77^{2,4}$	$2.97^{1,4,5,6} * 0.80^{2,3,4}$
Juvenile	0.5	x	0	0
SubAdult	0	0.5	x	0
Adult	0	0	$0.77^{2,4}$	$0.80^{2,3,4}$
Maximum				
Newborn	x	$0.67^{5} * 0.5$	$4.46^{1} * 0.83^{2}$	$4.46^{1} * 0.83^{2}$
Juvenile	0.5	x	0	0
SubAdult	0	0.5	x	0
Adult	0	0	0.83^{2}	0.83^{2}

Table 3.2: Stage-structured matrices used for pocket gophers reaching sexual maturity at nine months, showing probability that an individual within each stage will survive and move to the next stage and the fecundity (number of offspring) that an individual of each stage will produce

within a time step. Models based on minimum, mean (between min and max), and maximum values found in the literature are shown side by side. See Figure 2 for the life cycle diagram showing which probabilities are represented in each cell of the tables.([1]Loeb 1990, [2]Anderson & MacMahon 1981, [3]Daly & Patton 1986, [4]Howard & Childs 1959, [5]Scheffer 1938).

	Newborn	Juvenile	SubAdult	Adult
Minimum				
Newborn	x	0	$1.69^{1} * 0.66^{2}$	$1.69^{1} * 0.75^{3}$
Juvenile	0.5	x	0	0
SubAdult	0	0.5	x	0
Adult	0	0	0.66^{2}	0.75^{3}
Mean				
Newborn	x	$0.63^{1} * 0.50$	$2.97^{1,4,5} * 0.77^{2,4}$	$2.97^{1,4,5,6} * 0.80^{2,3,4}$
Juvenile	0.5	x	0	0
SubAdult	0	0.5	x	0
Adult	0	0	$0.77^{2,4}$	$0.80^{2,3,4}$
Maximum				
Newborn	x	$0.67^{5} * 0.5$	$4.46^{1} * 0.83^{2}$	$4.46^{1} * 0.83^{2}$
Juvenile	0.5	x	0	0
SubAdult	0	0.5	x	0
Adult	0	0	0.83^{2}	0.83^{2}

Table 3.3: Population matrices used for voles showing probability that an individual within each stage will survive and move to the next stage and the fecundity (number of offspring) that an individual of each stage will produce within a time step. Minimum, mean, and maximum values are shown side by side. See Figure 3 for an explanation of stage-structured models and which probabilities are represented in each cell of the tables. ([1]Beacham 1979, [2]Krebs 1966, [3]Boonstra & Krebs 1976, [4]Beacham 1979a, [5] Boonstra 1977a, [6]Krohne 1980, [7]Hoffman 1958, [8]Batzli & Pitelka 1971).

	Juvenile	Adult
Minimum		
Juvenile	$3.46^{6} * 0.20^{2}$	$3.46^{6} * 0.02^{1}$
Adult	0.20^{2}	0.02^{1}
Mean		
Juvenile	$5.02^{3} * 0.28^{1,2,8}$	$5.02^{3} * 0.35^{1,2,4,5,8}$
Adult	$0.28^{1,2,8}$	$0.35^{1,2,4,5,8}$
Maximum		
Juvenile	$6.56^{7} * 0.41^{8}$	$6.56^{7} * 0.51^{8}$
Adult	0.41^{8}	0.51^{8}

Table 3.4: Pocket gopher simulation scenarios.

Parameter or State Variable	High	Medium	Low
N_0 pocket gopher	K_{prey}	$0.5K_{prey}$	2
P	1	0.6	0.2
α	3	0.9	0.009
$K_{pocketgopher}$	175	100	25
$r_{pocketgopher}$	0.32	0.19	0.02
$r_{pocketgopherAnnual}$	1.28	0.76	0.08

Table 3.5: Vole simulation scenarios.

Parameter or State Variable	High	Medium	Low
N_0 vole	K_{prey}	$0.5K_{prey}$	2
P	1	0.6	0.2
α	3	0.9	0.009
K_{vole}	1000	500	50
r_{vole}	1.45	0.7	0.01
$r_{voleAnnual}$	5.8	2.8	0.04

References

Askham, L.R. 1988. "A two year study of the physical and economic impact of voles (Microtus montanus) on mixed maturity apple (Malus spp.) orchards in the Pacific Northwestern

United States." In *Proceedings of the 13th Vertebrate Pest Conference*, 151–55. University of California, Davis.

Baldwin, Roger A., Terrell P. Salmon, Robert H. Schmidt, and Robert M. Timm. 2014. "Perceived damage and areas of needed research for wildlife pests of California agriculture." *Integrative Zoology*, no. 9: 265–79. https://doi.org/10.1111/1749-4877.12067.

Batzli, George O., and Frank A. Pitelka. 1971. "Condition and Diet of Cycling Populations of the California Vole, Microtus californicus." *Journal of Mammalogy* 52 (1): 141–63.

Beacham, Terry D. 1979a. "Selectivity of avian predation in declining populations of the vole Microtus townsendii." *Canadian Journal of Zoology* 57: 1767–72.

———. 1979b. "Survival in Fluctuating Populations of the Vole Microtus-Townsendii." *Canadian Journal of Zoology* 57 (12): 2375–84. https://doi.org/10.1139/z79-309.

Boonstra, Rudy. 1977. "Predation on Microtus townsendii populations: impact and vulnerability." *Canadian Journal of Zoology* 55: 1343–1631. https://doi.org/10.1139/z77-212.

Byers, R.E. 1984. "Control and management of vertebrate pests in deciduous orchards of the eastern United States." *Horticulture Review* 6: 253–85.

Cantor, L., and T.G. Whitham. 1989. "Importance of belowground herbivory: pocket gophers may limit aspen to rock outcrop refugia." *Ecology* 70: 962–70.

Chitty, B Y Dennis, and Ellen Phipps. 1966. "Seasonal Changes in Survival in Mixed Populations of Two Species of Vole." *Journal of Animal Ecology* 35 (2): 313–31.

Clark, J. 1984. "Vole control in field crops." In *Proceedings of the Vertebrate Pest Conference*, 5–6.

Cockburn, A., and W.Z. Jr. Lidicker. 1983. "Microhabitat heterogeneity and population ecology of an herbivorous rodent, Microtus californicus." *Oecologia* 59: 167–77.

Cook, J.B. 1939. "Pocket gophers spread Canada thistle." *California Department of Agriculture Bulletin.* 28: 142–43.

Cudworth, Nichole L., and John L. Koprowski. 2010. "Microtus californicus (Rodentia: Cricetidae)." *Mammalian Species* 42 (June): 230–43. https://doi.org/10.1644/868.1.

Daly, J. C., and J. L. Patton. 1986. "Growth, Reproduction, and Sexual Dimorphism in Thomomys bottae Pocket Gophers." *Journal of Mammalogy* 67 (2): 256–65. https://doi.org/10.2307/1380878.

Howard, W.E., and H.E. Childs. 1959. "Ecology of pocket gophers with emphasis on Thomomys bottae mewa." *Hilgardia* 29: 277–358.

Jenkins, S.H., and P.W. Bollinger. 1989. "An experimental test of diet selection by the pocket gopher Thomomys-monticola." *Journal of Mammalogy* 70: 406–12.

Klemola, Tero, Minna Koivula, Erkki Korpimaki, and Kai Norrdahl. 1997. "Small Mustelid Predation Slows Population Growth of Microtus Voles : A Predator Reduction Experiment." *Journal of Animal Ecology* 66 (5): 607–14.

Korpimäki, Erkki, and Charles J. Krebs. 1996. "Predation and Population Cycles of Small Mammals : A Reassessment of the Predation Hypothesis." *Bioscience* 46 (10): 754–64. https://doi.org/10.2307/1312851.

Krebs, Charles J. 1966. "Demographic Changes in Fluctuating Populations of Microtus californicus." *Ecological Monographs* 36: 239–73.

Kross, Sara M., and Roger A. Baldwin. 2016. "Gopherbusters? A review of the candidacy of barn owls as the ultimate natural pest control option." In *27th Proceedings of the Vertebrate Pest Conference*. University of California, Davis.

Kross, Sara M., Ryan P. Bourbour, and Breanna L. Martinico. 2016. "Agricultural land use, barn owl diet, and vertebrate pest control implications." *Agriculture, Ecosystems and Environment* 223: 167–74. https://doi.org/10.1016/j.agee.2016.03.002.

Labuschagne, Lushka, Lourens H. Swanepoel, Peter J. Taylor, Steven R. Belmain, and Mark Keith. 2016. "Are avian predators effective biological control agents for rodent pest management in agricultural systems?" *Biological Control* 101: 94–102. https://doi.org/10.1016/j.biocontrol.2016.07.003.

Loeb, Susan C. 1990. "Reproduction and population structure of pocket gophers (Thomomys bottae) from irrigated alfalfa fields." *Proceedings of the Fourteenth Vertebrate Pest Conference 1990*, no. Paper 56.

Luce, D.G., R.M. Case, and J.L. Stubbendieck. 1981. "Damage to alfalfa fields by plains pocket gophers." *Journal of Wildlife Management* 45: 258–60.

Maher, William J. 1970. "The Pomarine Jaeger as a Brown Lemming Predator in Northern Alaska." *The Wilson Bulletin* 82 (2): 130–57. https://doi.org/10.2307/4159947.

Marsh, R.E. 1994. "Belding's, California, and Rock Ground Squirrels." In *The Handbook: Prevention and Control of Wildlife Damage*, edited by S.E. Hyngstrom, R.M. Timm, and G.E. Larson, B151–B158.

Merwin, I.A., J.A. Ray, and P.D. Curtis. 1999. "Orchard groundcover management systems affect meadow vole populations and damage to apple trees." *HortScience* 34: 271–74.

Miller, M.A. 1953. "Experimental studies on poisoning pocket gophers." *Hilgardia* 22: 131–66.

———. 1957. "Burrows of the Sacramento Valley pocket gopher in flood-irrigated alfalfa fields." *Hilgardia* 26: 431–52.

Miller, Milton A. 1946. "Reproductive Rates and Cycles in the Pocket Gopher." *Journal of Mammalogy* 27 (4): 335–58. https://doi.org/10.1644/870.1.Key.

Montazar, Aliasghar, Daniele Zaccaria, Khaled Bali, and Daniel Putnam. 2017. "A Model to Assess the Economic Viability of Alfalfa Production Under Subsurface Drip Irrigation in California." *Irrigation and Drainage* 66 (1): 90–102. https://doi.org/10.1002/ird.2091.

Murray, K.F. 1965. "Population changes during the 1957-1958 vole (Microtus) outbreak in California." *Ecology* 46: 163–71.

Nie, H., and J. Liu. 2005. "Regulation of root vole population dynamics by food supply and predation: a two-factor experiment." *Oikos* 109: 387–95.

Ordeñana, Miguel A., Dirk H. Van Vuren, and John P. Draper. 2012. "Habitat associations of California ground squirrels and Botta's pocket gophers on levees in California." *Journal of Wildlife Management* 76 (8): 1712–7. https://doi.org/10.1002/jwmg.402.

R Development Core Team. 2018. "R: A Language and Environment for Statistical Computing." Edited by R Development Core Team. R Foundation for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; R Foundation for Statistical Computing. https://doi.org/10.1007/978-3-540-74686-7.

Reichman, O.J., and S.C. Smith. 1985. "Impact of pocket gopher burrows on overlying vegetation." *Journal of Mammalogy* 66: 720–25.

Rinaldi, Sergio, Simona Muratori, and Yuri Kuznetsov. 1993. "Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities." *Bulletin of Mathematical Biology* 55 (1): 15–35. https://doi.org/10.1007/BF02460293.

Smallwood, K Shawn, Shu Geng, and Minghua Zhang. 2001. "Comparing pocket gopher (Thomomys bottae) density in alfalfa stands to assess management and conservation goals in northern California" 87: 93–109.

Smallwood, Shawn, and Shu Geng. 1997. "Multiscale influences of gophers on alfalfa yield and quality." *Field Crops Research* 49 (2-3): 159–68. https://doi.org/10.1016/S0378-4290(96)01034-9.

Stubben, C.J., and B.G. Milligan. 2007. "Estimating and Analyzing Demographic Models Using the popbio Package in R." *Journal of Statistical Software* 22 (11).

Sullivan, T.P., and E.J. Hogue. 1987. "Influence of orchard floor management on vole and pocket gopher populations and damage in apple orchards." *Journal of the American Society for Horticultural Science* 112: 972–77.

Witmer, Gary W., N.P. Snow, L. Humberg, and Terrell P. Salmon. 2009. "Vole problems, management options, and research needs in the United States." In *Proceedings of the Wildlife Damage Management Conference*, 235–49.

CHAPTER II:

DEMOGRAPHY AND ABUNDANCE OF NATIVE AND INVASIVE POPULATIONS OF A LARGE VERTEBRATE PEST

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Abstract:

Invasive species are a conservation concern because they pose a major threat to the functioning of ecosystems and the long-term persistence of biodiversity. The ecological processes that allow a species to become invasive in the first place may also allow them to grow to larger abundances or densities than they commonly would in their native range. Understanding how population characteristics differ between their native and invasive ranges can help scientists and conservation practitioners identify efficient strategies to manage or eradicate such species. Using wild pigs (*Sus scrofa*) as a case study, I compared the population demographic characteristics of native and invasive populations by conducting a global literature review and meta-analysis. I found that litter size, female adult survival, and subadult survival do not differ between the native range and the invaded range. However, juvenile survival is higher in the native range when compared to the invasive range. Population density was the only population parameter where habitat type and environmental parameters significantly explained differences between populations. Wild pigs are known to have large impacts on the environments they invade, but show few signs of differences in population characteristics,

suggesting that other processes such as predator density or behavioral plasticity may be more important in determining the extent of impact of species in invaded ranges.

Introduction

Species invasions were described by Elton (1958) as "population explosions" where species were able to proliferate, unchecked in new areas. Release from natural enemies (Crawley, 1987; Keane & Crawley, 2002; Noble, 1989), rapid evolution (Blossey & Notzold, 1995), filling of empty niches (Macarthur, 1970), and adaptation to novel disturbance (Baker, 1965) are some reasons that nonnative species have successfully expanded beyond their native range. These processes may allow invaders to outcompete their native counterparts or grow to higher abundances or densities than is commonly seen in their native ranges (Elton, 1958; Maron & Vilà, 2001). Comparing the demography of populations of native and invasive plant congeners, Ramula et al. (2008) found that invasive populations had higher population growth rates than their native counterparts. Additionally, abundance is considered a critical part of impact (Parker et al. 1999) and one of the most commonly used metrics to identify and classify a species as invasive (Catford et al., 2016). Use of population characteristics to classify a species as invasive suggests that the attributes are being compared to some baseline, though it is not always clear if the population baseline is the native population characteristics or the characteristics of other invasive populations.

Understanding if and how populations differ between the native and invaded ranges can help to identify ecological factors that may be responsible for higher population abundances or densities. For example, the pasture weed *Echium plantagineum* displays elevated seedling establishment and seed bank incorporation rates in its invasive range, resulting in much higher abundances than in its native range (Grigulis, Sheppard, Ash, & Groves, 2001). However, most studies that have undertaken comparative reviews of the population characteristics in the native

and invaded ranges focus on plants (for example Grigulis, Sheppard, Ash, & Groves, 2001; Hyatt & Araki, 2006; but see Bissattini & Vignoli, 2017; Parker et al., 2013). Further investigation into the dynamics of vertebrate species in the native versus invaded ranges is needed to understand if the same patterns of higher abundance and establishment rates that have been observed for plants in the invasive range exist for animals. Parker et al. (2013) found that for a subset of animals from the list of "100 of the World's Worst Invasive Alien Species", individuals in the invaded range were larger in body size and had slightly higher reproduction compared to counterparts in native ranges; but evidence of higher abundance in the invasive range was mixed. However, the authors did not measure other aspects that likely influence population dynamics like survival.

Demographic processes are a central component of invasive species management, as life history parameters are used to project the abundance and growth of many invasive populations to inform recommendations for management (Gurevitch, Fox, Wardle, Inderjit, & Taub, 2011; Kerr, Baxter, Salguero-Gómez, Wardle, & Buckley, 2016; I. M. Parker, 2000; Ramula et al., 2008). In particular, demographic models have been used to understand the efficacy of different management strategies for reducing invasive species abundance. Ramula et al. (2008) have proposed using demographic data to identify effective targets for reduction in population growth rates of invaders, practices which have been applied to a variety of plant species (see Dauer, McEvoy, & Van Sickle, 2012; Davis et al., 2012; Jiao, Lapointe, Angermeier, & Murphy, 2009 for examples). However this strategy of comparing native and invasive populations has not been broadly applied for vertebrates (but see Lurgi, Wells, Kennedy, Campbell, & Fordham, 2016; Wells et al., 2016 for application to European rabbit control), including wild pigs *(Sus scrofa)*.

This work contributes to our understanding differences between native and invasive vertebrate population characteristics and can provide insights to more efficiently manage

invasive vertebrate species. Using meta-analysis techniques, this paper provides a framework for assessing how vertebrate invasive species differ between the native and invasive ranges. I compare the demographic and population dynamics traits of native and invasive wild pig populations to evaluate if there are consistent differences between the populations. Because of more limited ecological controls in their invaded ranges, we predict that invasive species populations will be larger than in their invaded ranges and that this will be reflected in key life history transitions and population parameters. This meta-analysis will test whether invasive species populations are larger in the invaded range than the native range and will assess whether wild pigs occur at higher densities, have higher survival, or larger litter sizes in the invasive range.

Wild Pigs

Wild pigs have one of the largest geographic ranges and distributions of any large mammal globally (Figure 1), and are omnivorous (Fournier-Chambrillon, Maillard, & Fournier, 1995) habitat generalists (Oliver & Leus, 2008). They are native to Europe and Asia, with native populations extending to the Mediterranean basin, Eastern Russia, Japan, and Southeast Asia (Oliver & Leus, 2008). They have been driven to regional extinction in Denmark, Egypt, Ireland, Libya, parts of the UK, and Norway due to both hunting and habitat loss (Oliver & Leus, 2008). Recent efforts to rewild and rebuild native landscapes have resulted in their reintroduction in Sweden and the United Kingdom (Thurfjell et al., 2009). In North America, South America, Africa, Australia, and many oceanic islands wild pigs were introduced as a game species or for human consumption (Mayer & Brisbin, 1991).

The wild pig is considered one of the top 100 World's Worst Invaders (Lowe, Browne, Boudjelas, & De Poorter, 2000). Wild pigs are of concern because they have a significant

negative impact on the environment (Mayer & Brisbin, 2009), especially at the community and ecosystem level and to the services these ecosystems provide. Across the native and invasive range, wild pigs affect plant, animal, and fungal communities in addition to negatively impacting crops and serving as important vectors for disease transmission (Barrios-Garcia & Ballari, 2012; Bevins, Pedersen, Lutman, Gidlewski, & Deliberto, 2014; Bowman & McDonough, 1991; McClure, Burdett, Farnsworth, Sweeney, & Miller, 2018; Pech & Hone, 1988; Seward, VerCauteren, Witmer, & Engeman, 2004; Siemann, Carrillo, Gabler, Zipp, & Rogers, 2009). They may also facilitate secondary plant and animal invasions (Nuñez et al., 2013; Setter et al., 2002). However, none of these studies pair native and invasive populations to understand how impacts or populations differ between the native and invasive range. Understanding more about the differences between native and invasive vertebrate populations could help in identifying and managing negative impacts.

Wild pigs provide a useful case study to evaluate differences between the native and invaded ranges. The propagule pressure and introduction pathways for wild pigs are similar to other invasive ungulates that were introduced for agricultural or recreational purposes, such as axis deer (*Axis axis*) or red deer (*Cervus elaphus*; Forsyth & Duncan, 2001), suggesting that a comparative review of wild pig populations may provide insights for managing other large vertebrate invaders. Moreover, across both the native and invaded range, wild pigs represent an important recreational resource for sport hunting, and their populations are therefore closely monitored in both ranges. Their occupation of a variety of habitat types can allow us to gain insights into the role of habitat similarity in determining population trends.

To date, there are few analyses investigating differences between populations of wild pigs (but see Lewis et al., 2019 for a summary of past and present distributions in the US, 2017 for a summary of global populations; Massei et al., 2015 for a summary of populations across

Europe), and none that explicitly examine differences between the native and invasive ranges. Here I use the term 'invasive' for any non-native population of pigs regardless of whether impacts have been assessed for individual sites.

Methods

This study examines population differences between the native and invasive ranges in two ways: (1) I re-analyze the population density data collected by Lewis et al. (2017) to contrast native and invaded ranges. (2) I undertook a comprehensive literature review of wild pig demography studies to understand differences in population dynamic characteristics, including litter size, female adult survival, subadult survival, and juvenile survival. I compared unconditional means of density, litter size, and survivals in the native and invasive range. I specified four models for each population characteristic, incorporating invasive status, environmental variables, and habitat characteristics. Habitat characteristics were defined in three separate ways: (1) Habitat classifications as forest, agriculture, or other habitat; (2) Mediterranean or non-Mediterranean habitat; or (3) Mainland only analyses, dropping out all island populations.

Data Collection

Density Data

To assess the relationship between invasive status (defined as whether population was introduced or is within native range) and density, I used data collected and reported in the meta-analysis conducted by Lewis et al. (2017). The authors assessed biotic and abiotic factors predicting densities of wild pigs globally, but did not assess differences between native and non-native ranges. Lewis et al. (2017) reported average population densities (individuals/km^2), latitude and longitude of the location and the name of the study where the values were reported in the literature. I reviewed all available papers in the dataset, but some were not available or

published in non-English languages. Because covariate data that was used in the original Lewis analysis was not available, I used their reported locations as input coordinates to calculate and specified weather and habitat data (described below).

Demographic Data

To understand differences between population dynamic characteristics of wild pigs in their native and invaded ranges, I conducted a literature review of demographic parameters across wild pig populations and reviewed a total of 107 papers, reports, and dissertations. I found these by conducting searches using both Google Scholar and Web of Science in January 2018, using the terms Sus scrofa AND wild AND population AND demog* -medic*.[1] The Google Scholar search resulted in 400 results; after duplicates were removed 394 candidate papers remained. The Web of Science search was refined by selecting the following categories: ecology, biodiversity conservation, zoology, environmental sciences, biology, and environmental studies, resulting in 77 papers. Papers were then removed from the combined list of 471 papers if they were duplicates between the two search methods, did not contain population-level information, were non-English titles, had to do with other species, or were about a different subject than population level data (e.g. having to do with history, bioarcheology, domestication, or disease). To supplement the studies from this systematic search, I conducted a snowball sampling of the citation lists of reviewed papers, where citation lists of the relevant titles were recorded. Wild pigs are a hunted across both their native and invasive ranges, so wildlife agencies are largely responsible for their management, therefore I expected data describing population characteristics of population to be within both the peer reviewed literature and

[1] An initial search using the terms Sus scrofa AND population AND demography was used in google scholar and yielded over 9000 results, thus was determined to be too broad to capture papers of interest. The term -medic* was used to exclude papers relating to the medical field, as pigs are a typical model species used in biomedical research.

agency reports. To address this, I used both Google Scholar and Web of Science to capture agency reports and the scientific literature. Most of the data presented here is from wildlife journals, agency journals, and dissertations or theses. Many of the studies relied on hunter-reported statistics or samples.

I recorded the following demographic variables and their reported standard errors from each publication where it was reported: population density, female survival, subadult survival, juvenile survival, and mean litter size (Table 1). I reported survival for each stage as an annual rate, where the juvenile stage was defined as the first year of life, subadult as between one and two years, and adults as greater than one year. For studies that occurred over multiple years, I only recorded the reported standard errors of between year variability (not within year sampling error). Litter size was most commonly measured in terms of fetal counts from harvested females, observed juveniles, or counts of corpora lutea. I would expect estimated litter sizes calculated from copora lutea to be highest, followed by fetal counts, and observed juveniles to have the lowest size estimates. Data on number of litters per year was limited and therefore could not be controlled for in the models. To characterize the populations, I recorded size of study area, whether the population was hunted, and whether the population was native or invasive. Populations in the native and invasive range are both hunted, and I do not present population parameters of pigs under special controls outside of hunting in the invaded range. Reporting of standard errors, size of study area, and hunting of the population was uneven across studies, so I could not use these variables in my analyses.

Environmental Variables

Environmental and climatological characteristics have been shown to be important covariates determining the population dynamics of wild pig populations (Lewis et al., 2017).

Segura et al. (2014) showed that wild pig relative abundance was explained by wolf frequency, and environmental characteristics such as forest cover, temperature, and elevation. Because data were generally unavailable on predator populations for the many study regions, I focus here on climate variables and broad habitat descriptions.

Climate variables

Acevedo et al. (2006) showed that the abundance of wild pig populations is significantly related to temperature and landscape structure and diversity. Precipitation has also been shown to influence the breeding biology of wild pig populations in Mediterranean ecosystems (Fernández-Llario & Mateos-Quesada, 2005). To account for these relationships, I used the National Oceanic and Atmospheric Administration (NOAA) global summary of temperature and precipitation from the Climate Online Database (National Oceanic and Atmospheric Administration, 2019). I cropped the temperature and precipitation raster bricks to 1.5 x 1.5° blocks using the lat/long location as the centroid. I calculated the mean temperature in Celsius and mean precipitation in mm over the time the study took place plus ten previous years to account for longer term variability that can impact population dynamics. This same process was used to calculate mean temperature and precipitation for the locations given in the dataset taken from Lewis et al. (2017). In some cases, Lewis et al. (2017) calculated average densities for specific regions using multiple studies, in these cases, the period of time used to calculate the mean temperature and precipitation spanned ten years previous to the oldest study, ending at the publication year of the most recent study.

Habitat variables

Based on study site descriptions and dominant habitat type reported, I evaluated the potential role of habitat in several ways. First, I characterized the habitat as (1) forest, (2)

agricultural, or (3) 'other'. The Lewis et al. (2017) data set was categorized in the same way. For this analysis habitat was treated as a categorical variable and was dummy coded. Habitat classifications from the density data were not available, so I classified habitat based on study site descriptions or from site descriptions from studies occurring at the same site in a similar time period. Where neither of these were available, I used the Koppen-Geiger climate classification which gives a proxy for the type of habitat that may occur in a region (Beck et al., 2018), however this may not distinguish areas that were converted to agricultural habitat during that time period. This method was only used for 33 records in seven studies, from studies in Russia, Java, Belarus, Kazakhstan, and Azerbaijan.

Second, because populations occurring on islands are known to have fundamentally different dynamics from their mainland counterparts (Adler & Levins, 1994), I classified populations as island or mainland based on location and conducted a separate analysis. Island versus mainland was treated as a categorical variable and dummy coded.

Third because there is also a strong presence of wild pigs in Mediterranean habitats in both the native and invasive ranges, I also classified habitat as non-Mediterranean habitat or Mediterranean habitat based on the location of the study and its correspondence with habitat in the Csa, Csb, and Csc categories of the Koppen-Geiger climate classification (Beck et al., 2018). Wild pigs are known to be limited by hot temperatures and access to water (Baber & Coblentz, 1987), so Mediterranean climates may be a way to better understand how climate impacts population dynamics. The Mediterranean variable was also treated as a categorical variable and coded.

Statistical Analysis

I used t-tests to compare differences in unconditional means between native and invasive population densities, litter sizes, and survivals. I used generalized linear models to understand the role that invasive status plays in determining population characteristics of wild pig populations. Both litter size and density are continuous dependent variables bounded at zero, so I specified a model with a Gaussian distribution and log link function. Survival data is reported as a proportion and bounded between zero and one, therefore I specified a Gaussian distribution with a logit link function. In meta-analysis, standard errors are typically used to weight the dependent variable data, however uneven reporting of standard errors reduced sample size too much to be usable for weighting. Ectotherm performance typically has a quadratic dependence on temperature, so I used second degree centered orthogonal polynomials of temperature in all models. All analyses were carried out in R version 3.6.0 (R Development Core Team, 2018).

Four models were specified to examine differences in demographic parameters between the native and invasive populations; descriptions of each predictor variable can be found in Table 1. All analyses of litter size also included a categorical variable to control for how litter size was calculated. Model 1 included invasive status (native or invasive), average annual temperature, and average annual precipitation as predictor variables. Model 2 included the predictors from Model 1 and added a categorical habitat variable, classified as forest habitat, agricultural habitat, or other. Because there is a strong presence of Mediterranean habitat in both the native and invasive range, a third model was specified replacing the habitat variable in Model 2 with a classification of Mediterranean habitat for density and litter size. I was unable to conduct the Mediterranean analysis for survivals due to data limitations. Finally, given the unique population

dynamics that occur on islands, a fourth model was specified on mainland habitat only, using climate and habitat predictors. For all models, statistical significance is defined as $p < 0.05$.

Results

I reviewed 107 papers representing wild pig populations in 32 countries – seven countries in the invaded range and 25 in the native range (Figure 1). Most studies across both the native and invasive ranges occurred in forest habitat for both the demographic data and the density data (See Table 2 and 3 for a summary of the studies). Not all demographic parameters were reported by every study, so total number of populations differ for each analysis. All data from the literature is available on the Knowledge Network for Biocomplexity (KNB) repository.

Population density

Across all sites, the unconditional mean population density was significantly lower for native populations of wild pigs (2.83 pigs/km^2, SE = 0.55, N = 89) when compared to invasive populations (6.92 pigs/km^2, SE = 1.51, N = 40; $t = -2.55$ $p = 0.01$). When island sites were removed from the sample, the unconditional mean population density was 2.57 pigs/km^2 (SE = 0.49, N = 87) for native populations and 3.25 pigs/km^2 (SE = 0.44, N = 31) for invasive populations, and the populations were not significantly different ($t = -1.02$, $p = 0.31$).

Models 1 and 2, which differ in their fit by only 1.3 AIC units, show that invasive status has a positive, but not significant relationship with population density (Model 1: $\beta = 0.34$, $p = 0.14$; Model 2: $\beta = 0.35$, $p = 0.26$; Supplemental Table S1). They also show a significant positive relationship between precipitation and density. Model 2 shows that regions that are dominated by agricultural systems have a significantly positive relationship with density when compared to forested ecosystems ($\beta = 1.17$, $p = 0.002$). ANOVA shows that the total habitat variable for the

model is not significant ($p = 0.15$). Model 3, which incorporates Mediterranean habitat as a classifier, shows that Mediterranean habitat is not a significant predictors of density ($\beta_{mediterranean\ climate} = 0.38$, $p = 0.43$), and there is not a significant interaction between invasive status and being within a Mediterranean climate area ($\beta_{interaction} = 0.46$, $p = 0.37$). Finally, when the data are limited to only mainland populations, climate variables are no longer significant, and there is a negative relationship between invasive status and population density (Model 4: $\beta = -1.49$, $p = 0.01$). Non-forest, non-agricultural habitat has a negative relationship with density for native populations only ($\beta = -1.79$, $p = 0.04$), but this pattern is reversed and not significant when invasive status is interacted with habitat ($\beta = 0.68$, $p = 0.84$). ANOVA of Model 4 shows that the total habitat variable is not significant ($p = 0.78$)

Litter size

Unconditional mean litter size was significantly smaller for native populations (4.85 individuals per litter, SE = 0.21, N = 32) than invasive populations (5.57 individuals per litter, SE = 0.24, N = 27; $t = -2.28$, $p = 0.03$).This difference appears to be driven by the 6 island populations which if removed cause the relationship to be non-significant. For mainland populations, unconditional mean litter size was 4.85 individuals per litter (SE = 0.21, N = 32) in native populations and 5.44 individuals per litter (sd = 0.29, N = 21) for invasive populations, but the means were not significantly different ($t = -1.67$, $p = 0.10$). Models 1, 2, and 4 show positive, but not statistically significant relationships of litter size to invasive status (Model 1: $\beta = 0.11$, $p = 0.08$; Model 2: $\beta = 0.16$, $p = 0.07$; Model 4: $\beta = 0.18$, $p = 0.09$; Supplemental Table S2). Across all models, litter observation method exhibits patterns we would expect with negative coefficients for observed nests and positive or close to zero for corpora lutea counts when compared to fetus counts. Quadratic mean annual temperature has a positive and significant

relationship with litter size in Models 1 and 2 (see Supplement 2 for an explanation of this relationship), but this relationship was attenuated when accounting for Mediterranean habitat or subsetting to mainland observations. Habitat was not a significant predictor of litter size, however, there was a significant and negative relationship in the invaded range between litter size and Mediterranean habitats (β = -0.36, $p < 0.001$).

Survival:

Survival was assessed separately for female adults (greater than 2 years old), subadults (1-2 years old), and juveniles (<1 year old). There were no sites in the Mediterranean habitat in the invaded range that reported survival values for any stage, so the Mediterranean models are excluded.

Female Adult Survival

Unconditional mean female adult survival for the total sample were not significantly different between native (0.54/year, SE = 0.05, N = 16) and invasive populations (0.48/year, SE = 0.06, N = 18; t =0.80, p = 0.43). When the sample excluded island populations, mean survival was 0.54/year (SE = 0.05, N = 16) for native populations and 0.55 (SE = 0.07, N = 14) for invasive populations (t = -0.14, p = 0.89). Across all three models, the only significant coefficient is a negative relationship between quadratic mean annual temperature and female adult survival (Supplemental Table S3). There is a positive, but not statistically significant relationship between invasive status and female adult survival for all models (Model 1: β = 0.36, p = 0.39; Model 2: β = 0.22, p = 0.67; Model 3: β = 0.42, p = 0.50). Adding habitat parameters does not significantly influence female adult survival.

Subadult Survival

Unconditional mean subadult survivals for the total sample were not significantly different ($t = 1.66$, $p = 0.11$), the mean for native populations was 0.53/year (SE = 0.07, $N = 12$) and 0.40/year (SE = 0.04, $N = 11$) for invasive populations. Mainland populations alone were also not significantly different among native vs invaded ranges ($t = 1.08$, $p = 0.29$). For the subadult stage, models show that none of the modeled predictors have a significant relationship with subadult survival (Supplemental Table S4). Adjusted R^2 for all models show a poor fit of the predictors for the model.

Juvenile Survival

Unconditional mean juvenile survival was significantly higher in the native range (0.63/year, SE = 0.04, $N = 14$) than the invaded range (0.35/year, E = 0.04, $N = 17$; $t = 4.79$, $p = 3.44 \times 10^{-5}$) for the total sample. For native, mainland populations, the unconditional mean juvenile survival was also significantly higher (0.63/year, SE = 0.04, $N = 14$) than invasive populations (0.30/year, SE = 0.04, $N = 11$; $t = 5.32$, $p = 2.29 \times 10^{-5}$). Invasive status is significantly negatively related to juvenile survival for Models 1 and 2, and almost significant for Model 3 (Model 1: $\beta = -1.35$, $p < 0.001$; Model 2: $\beta = -0.84$, $p = 0.03$; Model 3: $\beta = -1.24$, $p = 0.07$; Supplemental Table S5). No other abiotic variables are significant predictors of juvenile survival.

Discussion

Population Differences

It is often assumed that invasive species achieve higher densities and have better demographic performance in the invaded range than in their native range. My meta-analysis of

107 population studies of the wild pig shows seems to support this assumption, with mean densities and litter sizes being larger in the invaded range. This appears to be due to differences in mean abiotic conditions across sites in the two ranges, instead of true differences in population densities. Using regression analysis to control for the effects of climate and habitat, I found that wild pig densities were lower in the invaded range than the native range (Model 4).

The only population characteristic that showed a significant relationship with invasive status was juvenile survival, which was lower in the invaded range than in the native range. This trend is opposite to the idea that invaders are successful because they are released from control by predators, parasites or competitors. It could be driven, in part, by anthropogenic reductions of the predators of wild pigs (such as bears and wolves) in the native range (Europe; Keuling et al., 2013). Recent efforts to reestablish large carnivore populations, including in Europe (Chapron et al., 2014), may reduce survival of wild pig populations, especially juveniles and subadults, in the future. Multiple studies have shown that wild pig densities are related to carnivore richness (Lewis et al., 2017; Segura et al., 2014). Future research will incorporate carnivore richness to assess the role of predators in determining the population dynamics of populations of wild pigs.

Habitat type (forest vs. agriculture vs. other) affected wild pig density but not demography. Both agricultural habitat and forested habitat are widely distributed in the native and the invasive ranges (Barrios-Garcia & Ballari, 2012), and populations of wild pigs are relatively well studied in these habitats. I found that agricultural habitat was positively associated with population density, in accord with prior studies showing that wild pigs use agricultural habitat as a reliable source of nutrient-dense food in both ranges (Ballari & Barrios-García, 2014). However; when an ANOVA was conducted on the model, the total habitat variable was not significantly related to population density ($p = 0.14$), suggesting that habitat is not an

important predictor for population density. Previous studies in the native range have shown that wild pig abundance is limited in agricultural systems occurring in lowland, arid environments because of lack of food and cover availability (Acevedo et al., 2006). Wild pig diets, however, have been shown to have significantly different compositions between the native and invaded ranges (Ballari & Barrios-García, 2014). It is unclear if these differences are driven by regional differences in the types of crops grown, control measures in place, or non-random study site selection.

The effect of biome (Mediterranean vs. non-Mediterranean) was not significantly related to litter size and density. Wild pigs are limited by hot summer temperatures and access to water, so control of invasive populations in Mediterranean habitats may be easier than in other habitats (Baber & Coblentz, 1986). However, there is not a significant interaction between invasive and native populations occurring in Mediterranean regions. More studies across ranges can allow us to model biome and habitat simultaneously to disentangle the differences between biome and habitat.

Populations occurring on island habitats are known to have unique dynamics that differ from their mainland counterparts (Adler & Levins, 1994), and on the island where they occur wild pigs have had strong effects on the local flora and fauna (Peart, Patten, & Lohr, 1994). While there are relatively few island populations represented in the data, dropping them from the models has a strong effect for density and juvenile survival. For density, when island populations are removed, invasive populations are shown to have a significantly lower population density for invasive populations than native populations. Therefore, accounting for differences in island and mainland impacts on population dynamics is important when comparing native and invasive populations. In contrast to density, when island populations are removed from the analysis of juvenile survival, the effect of invasive status becomes larger. This

suggests that juvenile survivals are lower for invasive populations on the mainland than their island counterparts. This makes sense because there are likely to be fewer predators in island habitats than mainland habitats.

Many populations of wild pigs have been recently reestablished and seem to be growing in size in the native range (Barrios-Garcia & Ballari, 2012; Goulding, Roper, Smith, & Baker, 2003; Keuling et al., 2013; Sandom, Hughes, & Macdonald, 2013); conversely, wild pig populations in the invasive range have been established for long periods of time, especially in the USA. Different lengths of establishment could be confounding the results and may contribute to the lack of differences observed. Separate models were run using initial year of study as a continuous variable to account for time since establishment, but it was not a significant predictor in any of the models. Studies across more of the range where wild pigs are distributed and more studies reporting demographic parameters could help to disentangle the role of establishment time, and the role of humans driving patterns in population dynamics of wild pig populations. There is much unexplained variance in all the models, suggesting that more nuanced assessments of climate, habitat, and incorporating other biotic variables can help to explain wild pig population dynamics.

Future Directions

The power, nuance, and generalities of my analyses were hindered by limitations in available data, including heterogeneity among studies in what was measured and reported. More uniform protocols for identifying and measuring population parameters such as survival and litter size could help identify how populations differ between the native and invasive range. Reporting of standard error terms can allow for the use of model weighting to better assess the relationships between abiotic variables and population characteristics, while accounting for gaps

in data. This study provides coarse-scale insights into the role of habitat in determining population outcomes, but more consistent reporting of habitat types in the literature can provide fodder for more robust analyses. Future analyses that make use of large databases such as Bioclim may be a way to better understand the role of habitat. Geographic biases in study location mean that there are gaps in our understanding of how wild pig populations in other regions might differ; more data collection on populations in South America, Asia, and Africa can help to generalize our knowledge of wild pig population dynamics. In this study, sites from the US were overrepresented in the invaded range, whereas sites from Spain and Italy were most common in the native range. Given that data span six continents, more specific continent-level analyses can provide a more robust understanding what drives this species to be successful globally. Finally, techniques from environmental history may be able to fill gaps in our understanding of when wild pig populations were established, and how they have persisted over time. The presence of demographic data in multiple places and at multiple time points suggests that wild pigs may be a good candidate for integrated assessment techniques to examine invasions risks across multiple spatial scales, allowing for rapid response to expanding populations (Ibanez et al., 2014).

Conclusion

This research highlights that common assumptions about differences between native and invasive populations may not hold in some taxa. Moreover, it suggests that any apparent increased performance by wild pigs in the invaded range, relative to the native range, can be explained by differences in site-specific conditions rather than invasive status. Therefore, habitat characteristics of the native range can be helpful predictors to understand where invasive vertebrates might thrive. It also gives managers insights to habitats that should be protected

from prior to invasion events to prevent successful establishment (such as agricultural habitats). This highlights the need to perform similar analyses of more invasive species to better understand whether (and under what circumstances) the assumption that species inherently perform better in the invaded range is warranted.

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References

Acevedo, P., Escudero, M. A., Muńoz, R., & Gortázar, C. (2006). Factors affecting wild boar abundance across an environmental gradient in Spain. *Acta Theriologica*, *51*(3), 327–336. https://doi.org/10.1007/BF03192685

Adler, G. H., & Levins, R. (1994). The Island Syndrome in Rodent Populations. *The Quarterly Review of Biology*, *69*(4), 473–490.

Baber, D. W., & Coblentz, B. E. (1986). Density, Home Range, Habitat Use, and Reproduction in Feral Pigs on Santa Catalina Island. *Journal of Mammology*, *67*(3), 512–525.

Baber, D. W., & Coblentz, B. E. (1987). Diet , Nutrition , and Conception in Feral Pigs on Santa Catalina Island. *The Journal of Wildlife Management*, *51*(2), 306–317.

Baker, H. G. (1965). Characteristics and mode of origin of weeds. In H. G. Baker & G. L. Stebbins (Eds.), *The genetics of colonizing species* (pp. 147–172). New York, NY: Academic Press.

Ballari, S. A., & Barrios-García, M. N. (2014). A review of wild boar Sus scrofa diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, *44*(2), 124–134. https://doi.org/10.1111/mam.12015

Barrios-Garcia, M. N., & Ballari, S. A. (2012). Impact of wild boar (Sus scrofa) in its introduced and native range: A review. *Biological Invasions*, *14*(11), 2283–2300. https://doi.org/10.1007/s10530-012-0229-6

Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future köppen-geiger climate classification maps at 1-km resolution. *Scientific Data*, *5*, 1–12. https://doi.org/10.1038/sdata.2018.214

Bevins, S. N., Pedersen, K., Lutman, M. W., Gidlewski, T., & Deliberto, T. J. (2014). Consequences associated with the recent range expansion of nonnative feral swine.

BioScience. https://doi.org/10.1093/biosci/biu015

Bissattini, A. M., & Vignoli, L. (2017). Let's eat out, there's crayfish for dinner: American bullfrog niche shifts inside and outside native ranges and the effect of introduced crayfish. *Biological Invasions*, *19*(9), 1–14. https://doi.org/10.1007/s10530-017-1473-6

Blossey, B., & Notzold, R. (1995). Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants: A Hypothesis. *Journal of Ecology*, *83*(5), 887–889.

Bowman, D., & McDonough, L. (1991). Feral pig (Sus scrofa) rooting in a monsoon forest wetland transition, northern Australia. *Wildlife Research*, *18*(6), 761–765.

Catford, J. A., Baumgartner, J. B., Vesk, P. A., White, M., Buckley, Y. M., McCarthy, M. A., & Alpert, P. (2016). Disentangling the four demographic dimensions of species invasiveness. *Journal of Ecology*, *104*(6), 1745–1758. https://doi.org/10.1111/1365-2745.12627

Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*(6216), 1517–1519. https://doi.org/10.1126/science.1257553

Crawley, M. J. (1987). What makes a community invasible? In A. J. Gray, M. J. Crawley, & P. J. Edwards (Eds.), *Colonization, Succession, and Stability* (pp. 429–453). Oxford: Blackwell Publishing Ltd.

Dauer, J. T., McEvoy, P. B., & Van Sickle, J. (2012). Controlling a plant invader by targeted disruption of its life cycle. *Journal of Applied Ecology*, *49*(2), 322–330. https://doi.org/10.1111/j.1365-2664.2012.02117.x

Davis, Adam, S., Landis, D. A., Douglas, A., Nuzzo, V., Blossey, B., Gerber, E., & Hinz, H. L. (2012). Demographic models inform selection of biocontrol agents for garlic mustard (Alliaria petiolata). *Ecological Applications*, *16*(0), 4–5. https://doi.org/10.1890/1051-0761(2006)016

Elton, C. S. (1958). *The Ecology of Invasions by Animals and Plants*. London, England: University of Chicago Press.

Fernández-Llario, P., & Mateos-Quesada, P. (2005). Influence of rainfall on the breeding biology of Wild boar (Sus scrofa) in a Mediterranean ecosystem. *Folia Zoologica*, *54*(3), 240–248.

Forsyth, D. M., & Duncan, R. P. (2001). Propagule Size and the Relative Success of Exotic Ungulate and Bird Introductions to New Zealand. *The American Naturalist*, *157*(6), 583. https://doi.org/10.2307/3079300

Fournier-Chambrillon, C., Maillard, D., & Fournier, P. (1995). Diet of the wild boar (Sus scrofa L.) inhabiting the Montpellier garrigue. *Journal of Mountain Ecology*, *3*, 174–179.

Goulding, M. J. M. J., Roper, T. J. T. J., Smith, G. G. C., & Baker, S. J. S. (2003). Presence of free-living wild boar Sus scrofa in southern England. *Wildlife Biology*, *9*(SUPPL. 1), 15–20. https://doi.org/10.2981/wlb.2003.059

Grigulis, K., Sheppard, a. W., Ash, J. E., & Groves, R. H. (2001). The comparative demography of the pasture weed Echium plantagineum between its native and invaded ranges. *Journal of Applied Ecology*, *38*(2), 281–290. https://doi.org/10.1046/j.1365-2664.2001.00587.x

Gurevitch, J., Fox, G. A., Wardle, G. M., Inderjit, & Taub, D. (2011). Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters*, *14*(4), 407–418. https://doi.org/10.1111/j.1461-0248.2011.01594.x

Hyatt, L. A., & Araki, S. (2006). Comparative population dynamics of an invading species in its native and novel ranges. *Biological Invasions*, *8*(2), 261–275. https://doi.org/10.1007/s10530-004-5572-9

Ibanez, I., Diez, J. M., Miller, L. P., Olden, J. D., Sorte, C. J. B., Blumenthal, D. M., … Lawler, J. J. (2014). Integrated assessment of biological invasions. *Ecological Applications*, *24*(1), 25–37.

Jiao, Y., Lapointe, N. W. R., Angermeier, P. L., & Murphy, B. R. (2009). Hierarchical

demographic approaches for assessing invasion dynamics of non-indigenous species: An example using northern snakehead (Channa argus). *Ecological Modelling*, *220*(13–14), 1681–1689. https://doi.org/10.1016/j.ecolmodel.2009.04.008

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.*, *17*(4), 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Kerr, N. Z., Baxter, P. W. J., Salguero-Gómez, R., Wardle, G. M., & Buckley, Y. M. (2016). Prioritizing management actions for invasive populations using cost, efficacy, demography and expert opinion for 14 plant species world-wide. *Journal of Applied Ecology*, *53*(2), 305–316. https://doi.org/10.1111/1365-2664.12592

Keuling, O., Baubet, E., Duscher, A., Ebert, C., Fischer, C., Monaco, A., … Thurfjell, H. (2013). Mortality rates of wild boar Sus scrofa L. in central Europe. *European Journal of Wildlife Research*, *59*(6), 805–814. https://doi.org/10.1007/s10344-013-0733-8

Lewis, J. S., Corn, J. L., Mayer, J. J., Jordan, T. R., Farnsworth, M. L., Burdett, C. L., … Miller, R. S. (2019). Historical, current, and potential population size estimates of invasive wild pigs (Sus scrofa) in the United States. *Biological Invasions*, *21*(7), 2373–2384. https://doi.org/10.1007/s10530-019-01983-1

Lewis, J. S., Farnsworth, M. L., Burdett, C. L., Theobald, D. M., Gray, M., & Miller, R. S. (2017). Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. *Scientific Reports*, *7*(1), 44152. https://doi.org/10.1038/srep44152

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database. *The Global Invasive Species Database*. The Invasive Species Specialist Group (ISSG). Retrieved from www.issg.org/booklet.pdf

Lurgi, M., Wells, K., Kennedy, M., Campbell, S., & Fordham, D. A. (2016). A Landscape

Approach to Invasive Species Management. *PloS One*, *11*(7), e0160417. https://doi.org/10.1371/journal.pone.0160417

Macarthur, R. H. (1970). Species Packing and Competitive Equilibrium of Many Species. *Theoretical Population Biology*, *1*, 1–11.

Maron, J. L., & Vilà, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, *95*(3), 361–373. https://doi.org/10.1034/j.1600-0706.2001.950301.x

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., … Náhlik, A. (2015). Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*, *71*(4), 492–500. https://doi.org/10.1002/ps.3965

Mayer, J. J., & Brisbin, I. L. (1991). *Wild Pigs in the United States* (1st ed.). Athens, GA: University of Georgia Press.

Mayer, J. J., & Brisbin, I. L. (Eds.). (2009). *Wild Pigs: Biology, Damage, Control Techniques, and Management*. *Savannah River National Laboratory*. Aiken, South Carolina. https://doi.org/10.1016/B978-0-08-024821-9.50009-3

McClure, M. L., Burdett, C. L., Farnsworth, M. L., Sweeney, S. J., & Miller, R. S. (2018). A globally-distributed alien invasive species poses risks to United States imperiled species. *Scientific Reports*, *8*(1), 5331. https://doi.org/10.1038/s41598-018-23657-z

National Oceanic and Atmospheric Administration. (2019). NOAA Climate Data Online.

Noble, I. R. (1989). Attributes of invaders and the invading process: terrestrial and vascular plants. In J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, & M. Williamson (Eds.), *Biological Invasions* (pp. 301–313). New York, NY: John Wiley & Sons, Ltd.

Nuñez, M. A., Hayward, J., Horton, T. R., Amico, G. C., Dimarco, R. D., Barrios-Garcia, M. N.,

& Simberloff, D. (2013). Exotic Mammals Disperse Exotic Fungi That Promote Invasion by Exotic Trees. *PLoS ONE*, *8*(6), 1–6. https://doi.org/10.1371/journal.pone.0066832

Oliver, W., & Leus, K. (2008). Sus scrofa. *The IUCN Red List of Threatened Species 2008*. https://doi.org/10.2305/IUCN.UK.2008.RLTS.T41775A10559847.en

Parker, I. M. (2000). Invasion Dynamics of Cytisus scoparius: A Matrix Model Approach. *Ecological Applications*, *10*(3), 726–743. https://doi.org/10.2307/2641041

Parker, J. D., Torchin, M. E., Hufbauer, R. A., Lemoine, N. P., Alba, C., Blumenthal, D. M., … Wolfe, L. M. (2013). Do invasive species perform better in their new range. *Ecology*, *94*(5), 1–8. https://doi.org/10.1890/12-1810.1

Peart, D., Patten, D. T., & Lohr, S. L. (1994). Feral Pig Disturbance and Woody Species Seedling Regeneration and Abundance beneath Coast Live Oaks (Quercus agrifolia) on Santa Cruz Island, California. *Fourth California Islands Symposium: Update on the Status of Resources*, (Sterner 1990), 313–322.

Pech, R. P., & Hone, J. (1988). A Model of the Dynamics and Control of an Outbreak of Foot and Mouth Disease in Feral Pigs in Australia. *Journal of Applied Ecology*, *25*(1), 63–77.

R Development Core Team. (2018). R: A Language and Environment for Statistical Computing. (R. D. C. Team, Ed.), *R Foundation for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://doi.org/10.1007/978-3-540-74686-7

Ramula, S., Knight, T. M., Burns, J. H., & Buckley, Y. M. (2008). General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *Journal of Applied Ecology*, *45*(4), 1124–1133. https://doi.org/10.1111/j.1365-2664.2008.01502.x

Sandom, C. J., Hughes, J., & Macdonald, D. W. (2013). Rewilding the Scottish Highlands: Do Wild Boar, Sus scrofa , Use a Suitable Foraging Strategy to be Effective Ecosystem

Engineers? *Restoration Ecology*, *21*(3), 336–343. https://doi.org/10.1111/j.1526-100X.2012.00903.x

Segura, A., Acevedo, P., Rodríguez, O., Naves, J., & Obeso, J. R. (2014). Biotic and abiotic factors modulating wild boar relative abundance in Atlantic Spain. *European Journal of Wildlife Research*, *60*(3), 469–476. https://doi.org/10.1007/s10344-014-0807-2

Setter, M., Bradford, M., Dorney, B., Lynes, B., Mitchell, J., Setter, S., … Moore, J. (2002). Pond apple - are the endangered cassowary and feral pig helping this weed to invade Queensland's Wet Tropics? In H. Jacob, J. Dodd, & J. Moore (Eds.), *13th Australian weeds conference: weeds '"threats now and forever?"'* (pp. 173–176). Perth: Plant Protection Society of Western Australia Inc.

Seward, N. W., VerCauteren, K. C., Witmer, G. W., & Engeman, R. M. (2004). Feral swine impacts on agriculture and the environment. *Sheep and Goat Research Journal*, *19*(October), 34–40. Retrieved from http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1011&context=icwdmsheepgoat

Siemann, E., Carrillo, J. a, Gabler, C. a, Zipp, R., & Rogers, W. E. (2009). Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. *Forest Ecology and Management*, *258*(5), 546–553. https://doi.org/10.1016/j.foreco.2009.03.056

Thurfjell, H., Ball, J. P., Åhlén, P.-A., Kornacher, P., Dettki, H., & Sjöberg, K. (2009). Habitat use and spatial patterns of wild boar Sus scrofa (L.): agricultural fields and edges. *European Journal of Wildlife Research*, *55*(5), 517–523. https://doi.org/10.1007/s10344-009-0268-1

Wells, K., Cassey, P., Sinclair, R. G., Mutze, G. J., Peacock, D. E., Lacy, R. C., … Fordham, D. a. (2016). Targeting season and age for optimizing control of invasive rabbits. *The Journal of Wildlife Management*, 1–10. https://doi.org/10.1002/jwmg.21093

Figures

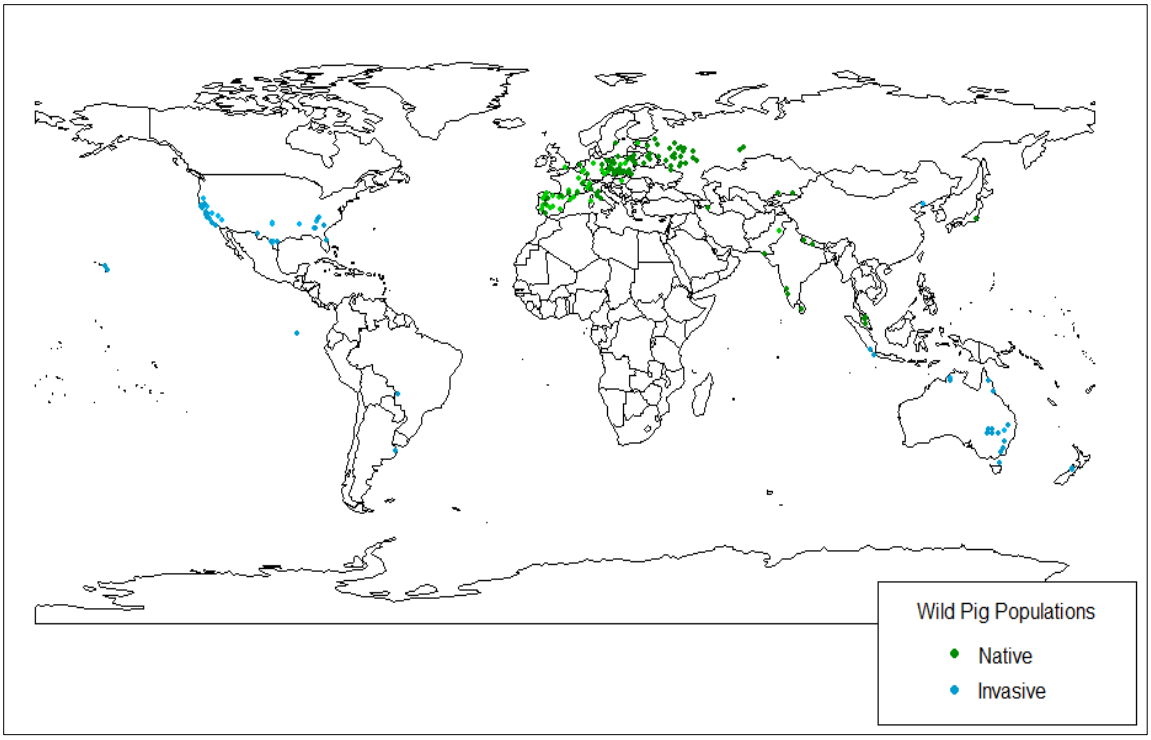

Figure 1: Distribution of studies where green points represent studies in the native range and blue points represent studies in the invaded range. Darker points indicate studies from the Lewis et al. (2017) data set used to characterize density. Twenty-Five studies from the native populations are represented: Azerbaijan, Belarus, Czech Republic, England, Estonia, France, Germany, Hungary, India, Italy, Japan, Kazakhstan, Lithuania, Luxembourg, Malaysia, Nepal, Netherlands, Pakistan, Poland, Portugal, Russia, Spain, Sri Lanka, Sweden, and Switzerland. In the invasive range, seven countries are represented: Argentina, Australia, Brazil, Ecuador, Indonesia, New Zealand, and the United States.

Tables

Table 1: Generalized Linear Model (glm) predictor variables and summary of models. Note that the analyses of litter size includes a categorical variable specifying which observation method was used to calculate the litter size. The dependent variable for each model is population density, litter size, female adult survival, subadult survival, or juvenile survival. Note that the predictor variable of litter type is only used in the models where litter size is the dependent variable.

Predictor Variable	Codes	Description
Invasive Status	Invasive	Whether the population is in the native or invasive range 0 = Native 1 = Invasive
Climate	MeanTemp	Mean Annual Temperature (°C)
	MeanPrecip	Mean Annual Precipitation (mm)
Habitat	Hab	Dominant Habitat Type 1 = Agricultural or agricultural/natural interface 2 = Forest (deciduous, oak, coniferous, tropical, mixed hardwood, and temperate forest are all represented) 3 = Other (Non-agricultural, non-forest)
Biome	MedHab	Mediterranean Habitat 0 = non-Mediterranean habitat 1 = Mediterranean habitat
Litter Observation Method	LitterType	How litter type was calculated 1 = Counts of fetuses 2 = Observed nests of newborns 3 = Counts of corpora lutea

Model	
1	~ Invasive + poly(MeanTemp, 2)+ MeanPrecip (+ LitterType)
2	~ Invasive + poly(MeanTemp, 2) + MeanPrecip + Hab (+ LitterType) (+ Hab x Invasive)
3	~ Invasive + poly(MeanTemp, 2) + MeanPrecip + MedHab (+ LitterType) (+ MedHab x Invasive)
4	Same as Model 2, but subsetted to mainland habitats

Table 2: Mean environmental characteristics for demographic data sites.

	Native Range	Invaded Range
Mean temp (°C)	12.5 (3.86)	17.0 (4.77)
Mean Min temp (°C)	-1.42 (6.03)	4.40 (7.14)
Mean Max temp (°C)	25.9 (3.18)	28.5 (4.10)
Mean precip (mm)	62.6 (16.4)	75.4 (34.0)
Mean Min precip (mm)	0.78 (1.41)	0.35 (1.61)
Mean Max precip (mm)	336.0 (94.8)	444.0 (167.0)
% forested sites	66.7%	59.6%
% agriculture sites	28.3%	14.9%
% non-forest, non-agricultural sites	5.0%	25.5%
% Island	0%	12.8%
% Mediterranean	58.3%	21.3%
Total number of observations	60	47

For temperature and precipitation, "Mean" is the mean across all site-specific means, whereas "Min" and "Max" are the means of the minimum annual means and maximum annual means. Standard deviations for the means are included in the parentheses.

Table 3: Mean environmental characteristics for demographic data sites for density data from Lewis et al. (2017).

	Native Range	Invaded Range
Mean temp (°C)	10.0 (6.32)	17.7 (5.24)
Mean Min temp (°C)	-6.94 (11.3)	8.11 (7.36)
Mean Max temp (°C)	24.4 (3.54)	26.7 (4.04)
Mean precip (mm)	67.7 (40.6)	80.0 (55.9)
Mean Min precip (mm)	1.78 (1.79)	0.39 (1.90)
Mean Max precip (mm)	335.0 (298.0)	484.0 (271.0)
% forested sites	86.6%	27.5%
% agriculture sites	6.7%	17.5%
% non-forest, non-agricultural sites	6.7%	55.0%
% Island	0%	22.5%
% Mediterranean	13.5%	27.5%
Total number of observations	89	40

For temperature and precipitation, "Mean" is the mean across all site-specific means, whereas "Min" and "Max" are the means of the minimum annual means and maximum annual means. Standard deviations for the means are included in the parentheses.

Supplemental Information: Regression Tables

Table S1: Summary of generalized linear models of relationship between wild pig populations density and abiotic predictor variables. All models specify a Gaussian distribution with a log-link function. Adjusted R^2's were calculated using variance-function-based values. For Model 2, the total p-value for ecosystem habitats was 0.14, and the total interactive term for status*ecosystem was 0.08. Note that the sample size is smaller for mainland population model. Invasive populations are compared against native populations and habitat variables are compared against forested habitats. Mediterranean habitat is compared against non-Mediterranean habitat.

Density Models

Predictor Variables	**Model 1: Clim.**			**Model 2: Clim. + Hab.**			**Model 3: Clim. + Med.**			**Model 4: Mainland**		
	Coef	SE	*p*	Coef	SE	*p*	Coef	SE	*p*	Coef	SE	*p*
Mean Annual Temp (C)	3.81	2.38	0.11	4.27	2.32	0.07	7.01	3.19	0.03	8.78	1.92	1.31×10^{-5}
Quadratic Mean Annual Temp (C)	-3.09	2.09	0.14	-1.78	2.02	0.38	-2.08	2.44	0.40	1.97	1.31	0.13
Mean Annual Precip (mm/year)	0.007	0.002	0.002	0.006	0.002	0.002	0.005	0.002	0.02	-0.004	0.003	0.15
Invasive Populations	0.34	0.23	0.14	0.35	0.31	0.26	0.19	0.26	0.47	-1.49	0.58	0.01
Agricultural Habitat (0/1)				1.17	0.38	0.002				0.51	0.45	0.26
Non-Forest and Non-Agricultural Habitat (0/1)				-0.03	1.06	0.98				-1.79	0.87	0.04
Invasive * Agricultural Habitat				-1.58	0.93	0.09				-0.36	0.81	0.66

Invasive * Non-Forest and Non-Agricultural Habitat				0.44	1.09	0.68				2.47	1.06	0.02
Mediterranean Climate							0.38	0.48	0.43			
Invasive * Mediterranean Climate							0.46	0.51	0.37			
Constant	0.62	0.32	0.05	0.42	0.36	0.24	0.54	0.40	0.18	1.28	0.29	2.97×10^{-5}
Observations	129			129			129			118		
Adjusted R^2	0.19			0.22			0.24			0.34		
Log Likelihood	-420.26			-414.61			-417.62			-310.72		
Akaike Inf. Crit.	850.52			849.22			851.23			641.43		

Table S2: Summary of generalized linear models of relationship between wild pig litter size and abiotic predictor variables. All models specify a Gaussian distribution with a log-link function. Adjusted R2's were calculated using variance-function-based values. For all models, the litter type variable is always significant (Model 1: $p = 1.70 \times 10^{-5}$; Model 2: $p = 0.0002$; Model 3: $p = 1.55 \times 10^{-6}$; Model 4: $p = 0.0003$). For Models 2 and 4, the neither total habitat variable nor the interaction term are significant (Model 2: $p = 0.64, 0.54$; Model 4: $p = 0.54, 0.62$) Note that the sample size is smaller for mainland population model. Invasive populations are compared against native populations and habitat variables are compared against forested habitats. Mediterranean habitat is compared against non-Mediterranean habitat.

Litter Size Models

Predictor Variables	**Model 1: Clim.**			**Model 2: Clim. + Hab.**			**Model 3: Clim. + Med.**			**Model 4: Mainland**		
	Coef.	SE	*p*	Coef.	SE	*p*	Coef.	SE	*p*	Coef.	SE	*p*
Mean Annual Temp (C)	0.07	0.21	0.74	-0.006	0.23	0.98	0.09	0.21	0.65	-0.12	0.24	0.62
Quadratic Mean Annual Temp (C)	0.40	0.19	0.04	0.40	0.20	0.05	-0.13	0.20	0.51	0.27	0.21	0.22
Mean Annual Precip (mm/year)	0.0002	0.001	0.88	0.0003	0.001	0.81	-0.002	0.001	0.06	-0.0002	0.002	0.89
Invasive Populations	0.11	0.06	0.08	0.16	0.09	0.07	-0.003	0.07	0.96	0.18	0.10	0.09
Observed nests	-0.51	0.14	0.0005	-0.50	0.15	0.001	-0.50	0.12	0.0001	-0.50	0.15	0.002
Corpora Lutea counts	0.02	0.07	0.74	0.04	0.07	0.58	-0.08	0.06	0.19	0.05	0.08	0.53
Agricultural Habitat (0/1)				0.11	0.08	0.17				0.12	0.09	0.17
Non-Forest and Non-Agricultural Habitat (0/1)				0.10	0.18	0.58				0.10	0.19	0.61
Invasive*Agricultural Habitat				-0.17	0.16	0.31				-0.19	0.23	0.40

Invasive*Non-Forest and Non-Agricultural Habitat				-0.11	0.21	0.61				-0.12	0.22	0.60
Mediterranean Climate							-0.36	0.08	4.11×10^{-5}			
Invasive*Mediterranean Climate							0.07	0.15	0.64			
Constant	1.61	0.08	$<2 \times 10^{-16}$	1.56	0.10	$<2 \times 10^{-16}$	1.98	0.10	$< 2 \times 10^{-16}$	1.58	0.13	1.0×10^{-15}
Observations	59			59			59			53		
Adjusted R^2	0.37			0.35			0.55			0.30		
Log Likelihood	-79.99			-78.73			-68.71			-71.78		
Akaike Inf. Crit.	175.99			178.96			157.42			167.56		

Table S3: Summary of generalized linear models of relationship between wild pig female adult survival and abiotic predictor variables. All models specify a Gaussian distribution with a log-link function. Adjusted R^2's were calculated using variance-function-based values. For Model 2, there were no records for native female survivals in non-forest, non-agricultural habitat, so the interaction between invasive status and habitat was not included. $P = 0.89$ for the total habitat variable in Model 2 and 0.85 for Model 3. Note that the sample size is smaller for mainland population model.

Female Adult Survival Models

Predictor Variables	**Model 1: Climate**			**Model 2: Climate + Habitat**			**Model 3: Mainland**		
	Coef.	SE	*p*	Coef.	SE	*p*	Coef.	SE	*p*
Mean Annual Temp (C)	-2.06	1.21	0.09	-1.87	1.34	0.17	-1.13	1.31	0.39
Quadratic Mean Annual Temp (C)	-2.94	1.00	0.006	-3.01	1.05	0.008	-2.19	1.05	0.05
Mean Annual Precip (mm/year)	-0.01	0.006	0.11	-0.009	0.008	0.27	-0.01	0.009	0.27
Invasive Populations	0.36	0.41	0.39	0.22	0.52	0.67	0.42	0.61	0.50
Agricultural Habitat (0/1)				0.13	0.47	0.78	0.30	0.53	0.58
Non-Forest and Non-Agricultural Habitat (0/1)				0.26	0.66	0.69	0.15	0.73	0.84
Constant	0.66	0.48	0.18	0.66	0.59	0.35	0.74	0.65	0.27
Observations	34			34			30		
Adjusted R^2	0.27			0.22			0.01		
Log Likelihood	8.94			9.08			6.77		
Akaike Inf. Crit.	-5.88			-7.73			2.45		

Table S4: Summary of generalized linear models of relationship between wild pig subadult survival and abiotic predictor variables. All models specify a Gaussian distribution with a log-link function. Adjusted R^2's were calculated using variance-function-based values. For Model 2, there were no records for native subadult survivals in non-forest, non-agricultural habitat, so the interaction between invasive status and habitat was not included. $P = 0.30$ for the total habitat variable in Model 2 and 0.19 for Model 3. Note that the sample size is smaller for mainland population model.

SubAdult Survival Models

Predictor Variables	**Model 1: Clim.**			**Model 2: Climate + Habitat**			**Model 3: Mainland**		
	Coef.	SE	*p*	Coef.	SE	*p*	Coef.	SE	*p*
Mean Annual Temp (C)	-0.41	1.13	0.67	-0.21	1.50	0.95	-0.23	1.48	0.79
Quadratic Mean Annual Temp (C)	-0.83	0.90	0.38	-1.26	0.97	0.21	-1.09	1.13	0.35
Mean Annual Precip (mm/year)	0.005	0.008	0.58	-0.0002	0.01	0.98	-0.005	0.01	0.73
Invasive Populations	-0.49	0.47	0.31	-0.29	0.71	0.69	0.29	0.94	0.76
Agricultural Habitat (0/1)				0.88	0.66	0.20	1.60	1.10	0.17
Non-Forest and Non-Agricultural Habitat (0/1)				-0.37	0.89	0.68	-0.88	1.08	0.43
Constant	-0.27	0.63	0.67	-0.05	0.76	0.95	0.25	0.95	0.79
Observations	23			23			19		
Adjusted R^2	-0.02			0.005			-0.07		
Log Likelihood	5.89			7.49			5.45		
Akaike Inf. Crit.	0.23			1.03			5.10		

Table S5: Summary of generalized linear models of relationship between wild pig juvenile survival and abiotic predictor variables. All models specify a Gaussian distribution with a log-link function. Adjusted R^2's were calculated using variance-function-based values. For Model 2, there were no records for native subadult survivals in non-forest, non-agricultural habitat, so the interaction between invasive status and habitat was not included. $P = 0.09$ for the total habitat variable in Model 2 and 0.67 for Model 3. Note that the sample size is smaller for mainland population model.

Juvenile Survival Models

Predictor Variables	**Model 1: Climate**			**Model 2: Climate + Habitat**			**Model 3: Mainland**		
	Coef.	SE	*p*	Coef.	SE	*p*	Coef.	SE	*p*
Mean Annual Temp (C)	0.74	0.82	0.38	-0.12	0.95	0.13	0.42	1.19	0.73
Quadratic Mean Annual Temp (C)	0.56	0.68	0.41	0.32	0.64	0.62	0.26	0.76	0.73
Mean Annual Precip (mm/year)	0.004	0.005	0.46	-0.002	0.005	0.69	0.0002	0.009	0.98
Invasive Populations	-1.35	0.32	0.0002	-0.84	0.37	0.03	-1.24	0.66	0.07
Agricultural Habitat (0/1)				0.29	0.38	0.45	0.03	0.46	0.95
Non-Forest and Non-Agricultural Habitat (0/1)				-1.05	0.58	0.09	-0.72	0.83	0.40
Constant	0.34	0.40	0.41	0.63	0.40	0.13	0.54	0.61	0.39
Observations	31			31			25		
Adjusted R^2	0.43			0.48			0.48		
Log Likelihood	16.57			19.44			14.01		
Akaike Inf. Crit.	-21.14			-22.88			-12.02		

Supplemental Information: Relationship between temperature and litter size

Temperature has been shown to have a quadratic relationship with ectotherms, suggesting that there should be an optimal range of temperatures over which population parameters should be highest, while extreme low and extreme high temperatures are not optimal. This creates a concave relationship between population variables and temperature like I saw for female adult survival (Figure S2.1)

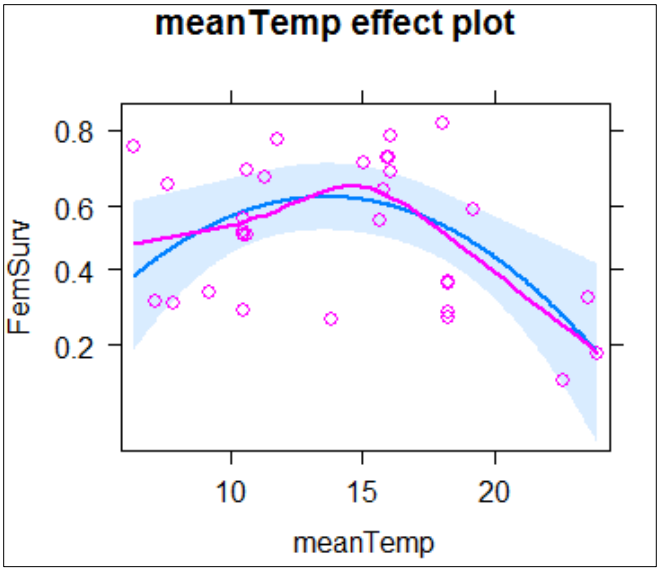

Figure S2.1: Component and partial residual plots for the quadratic transformed and orthogonal centered temperature with the Component and residuals for female adult survival. The blue line represents the fitted effect of temperature and the circles represent the residual deviation from the fit (after accounting for other variables in the model).

In the models assessing the relationship between litter size and climate variables (Model 1) and litter size and climate variables + habitat (Model 2), there is a significant positive relationship (Figure S2.2). Model 3, which includes Mediterranean climate instead of habitat variables show the relationship I would expect. Model 4, which is subsetted to only mainland populations shows a slightly concave relationship. Partial residual plots show that the convex curvature of the relationship is very shallow and likely an artifact of the limited amount of data available.

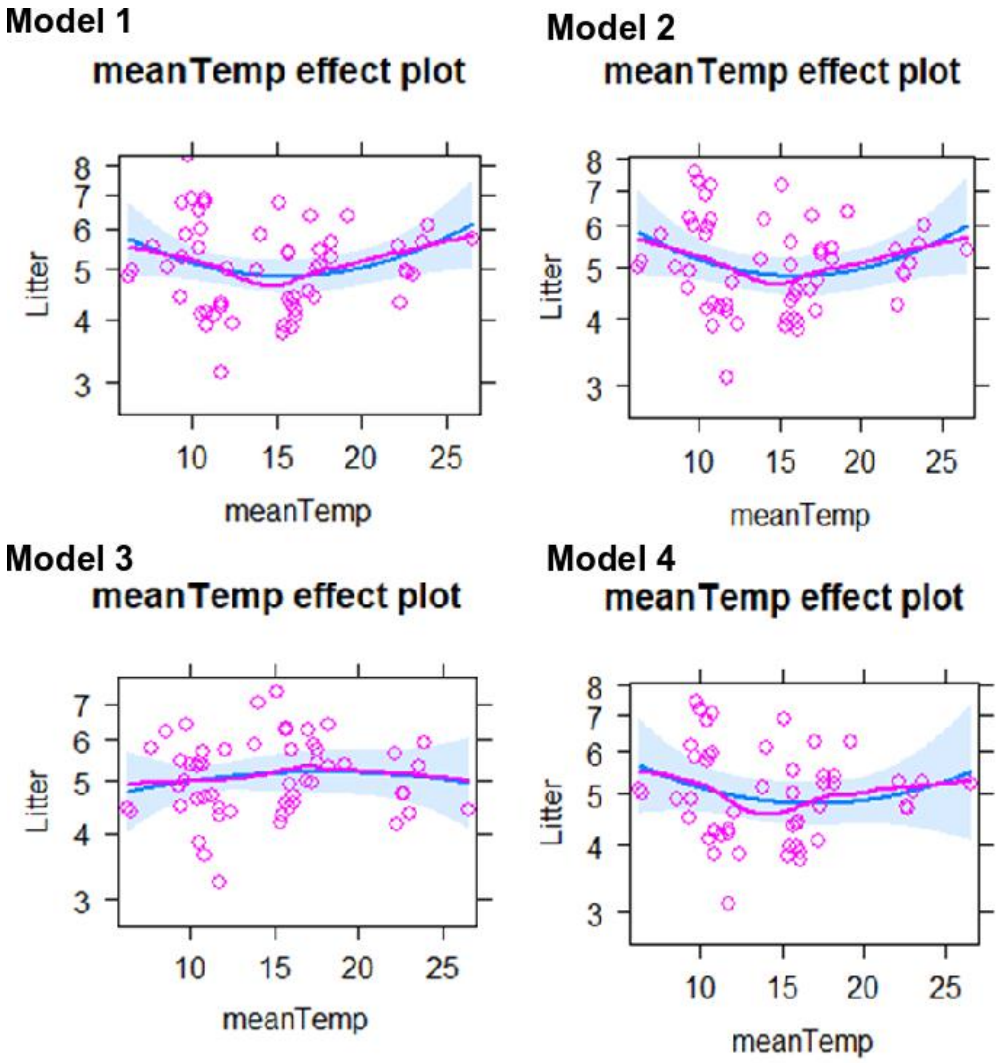

Figure S2.2: Component and partial residual plots for the quadratic transformed and orthogonal centered temperature with the Component and residuals for Litter size. The blue line represents the fitted effect of temperature and the circles represent the residual deviation from the fit (after accounting for other variables in the model).

CHAPTER III:

EFFECTS OF MESSAGE FRAMES ON SUPPORT FOR MANAGEMENT OF CLIMATE-DRIVEN SPECIES INVASIONS

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Abstract

Invasive species are an enduring problem globally; they are one of the biggest threats to biodiversity and have significant economic impacts. Public support for environmental policies can determine which get adopted and how quickly they are rolled out, thereby determining their effectiveness. As a result, understanding ways to increase support for such policies is important for managers implementing them. Here we test how support for invasive species management varies depending on what the message conveys about how the species was introduced. These different messages represent varying levels of responsibility that humans have for the presence of an invasive species in California. We show that message frames that attribute responsibility for invasive species presence to humans result in the highest levels of support for eradication programs. Meanwhile, frames that attribute responsibility to climate change have the lowest levels of support, for both non-environmentalists and environmentalists. These findings suggest that climate change-driven shifts in invasive species distributions may not serve as a compelling case to justify eradication programs. Where appropriate, human responsibility for introduction of invasive species should instead be highlighted to increase public support.

Introduction

Climate change is driving major changes to the global environment. Changes in temperature, precipitation, and frequency of extreme events are reshuffling and restructuring ecosystems across the globe (Pecl et al., 2017), making it is increasingly important to implement policies that mitigate the impacts associated with climate change. However, low public support for environmental policies can cause them to stall or can prevent their implementation (Beierle, 1999; Eden, 1996). To mitigate this, messages about environmental policies can be framed to increase public support for them by, for example, emphasizing climate change as a source of problems. This paper uses the case of invasive species management, where the source of responsibility for the problem can plausibly be attributed to humans, to the ecosystem, or to climate change, to assess whether attribution of responsibility is an effective way to increase support.

Species Invasions

Invasive species are species that are not native to the place they are found, and they cause damage or have the potential to cause damage in that place (Executive Order No. 13112, 1993; United Nations, 1992). Invasive species are introduced through human-mediated release of species or through natural dispersal from a neighboring area (Hulme et al., 2008). Beyond the initial introduction of a species, climate change is now driving shifts in invasive species distribution (Menéndez, González-Megías, Lewis, Shaw, & Thomas, 2008). Climate-driven poleward and upslope range shifts have been observed across a variety of taxa and in a variety of environments (Parmesan, 1996; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). In developed countries, risk of invasion from novel species is highest in places that coincide with climate-driven shifts in biomes (Early et al., 2016). Reshuffling and geographic expansion of

species populations have acute consequences for the environment and introduce the potential for new conflicts between humans and wildlife.

Invasive species are one of the most important drivers of environmental change and declines in global biodiversity (Chapin et al., 2000; Mack & D'Antonio, 1998). Almost half of endangered species in the US are at risk as a result of invasive species impacts (Wilcove et al. 1998). But invasive species also have significant economic impacts and are estimated to cost $120 billion annually in management and mitigation costs in the US (Pimentel, Lach, Zuniga, & Morrison, 2000; Pimentel, Zuniga, & Morrison, 2005).

Despite the problems associated with invasive species, it can be difficult to motivate the public to support invasive species management because it often involves culling of populations (McNeely, 2001; D. A. Simberloff, Parker, & Windle, 2005). Invasive species management programs can be halted or significantly delayed as a result of public opposition to them (Bremner & Park, 2007). This can have significant impacts on both natural ecosystems and managed areas, including agriculture. To mitigate this, message framing has been shown to be an effective tool at increasing public support for management proposals. For example, DeGolia et al. (2019) have shown that highlighting the ecological losses that are likely to occur from allowing invasive wild pigs (*Sus scrofa*) to proliferate and spread significantly increased support for their eradication. Here, we extend our understanding of the effectiveness of alternative message framing by examining a different attribute, perceived responsibility for introduction, affects support.

Attribute Framing

Frames are unconscious structures that communicate information about a particular subject and how it relates to other subjects or objects; they are implicit in any form of communication (Lakoff, 2010). Effective frames typically connect issues to people's core

concerns or beliefs (Nisbet, Markowitz, & Kotcher, 2012). Attribute frames are message frames that are used to highlight certain aspects of an object, which often affect the way a person evaluates that object (Levin, Schneider, & Gaeth, 1998). Using attribute framing when communicating with the public about environmental problems can influence attitudes and behavioral intentions (Davis, 1995). For example, Hardisty et al. (2010) examined the role of attribute framing in support for energy efficiency policy and found that framing the proposed policy as an allowance resulted in more support for the policy than when it was framed as a tax. For invasive species management, DeGolia et al (2019) found that highlighting the ecological impacts of invasive species increased support for eradication programs for wild pigs.

Support for environmental policies and attribution of responsibility

Message frames that highlight who or what is responsible for environmental problems may be one way to increase support for proposed solutions. Previous research has shown there is greater motivation to intervene in a problem that is caused by intentional human actions (Markowitz & Shariff, 2012), regardless of whether or not they intended to cause damage (Böhm & Pfister, 2000). For climate change, belief that humans are responsible for increasing CO_2 emissions is an important determinant of support for climate change mitigation policies (Malka, Krosnick, & Langer, 2009; Spence, Poortinga, Butler, & Pidgeon, 2011). In another study, Kaiser et al. (1999) found that feelings of responsibility toward the environment were an important predictor of pro-environmental behavior intentions. Individuals also perceive risks or hazards more negatively when they have been found to be caused by humans instead of natural processes, such as a human caused oil spill versus a natural disaster resulting in the release of oil into natural systems (Böhm & Pfister, 2000; Siegrist & Sütterlin, 2014), which can further motivate the public to act.

In contrast, people are less supportive of policies that mitigate processes that occur without direct human intervention, because they are perceived to be natural processes that do not require intervention (Böhm & Pfister, 2000). Moreover, situations where nature is responsible seem more uncontrollable to people, therefore they are less likely to take action (Bandura, 1977; Ferguson & Branscombe, 2010; Weiner, 1993). In flood risk management, the public recognizes that it is the responsibility of humans to guard themselves against the hazards associated with floods; but this assignment of responsibility is not necessarily associated with increased support of flood risk policies or adaptation measures because floods are perceived to be part of natural cycles in the environment (Bichard & Kazmierczak, 2012; Butler & Pidgeon, 2011). Attribution to human drivers for non-politicized environmental problems is likely to induce more support for intervention policies than when problems are attributed to natural causes, but clarifying this relationship for a broader range of environmental problems can provide important insights to the types of messages that can increase support for management.

Attribution of responsibility for species introductions

The different introduction pathways for species introductions can be leveraged to test the importance of attributed responsibility in determining public support for invasive species management (D. S. Simberloff, Parker, & Windle, 2005). Drivers of responsibility for invasive species introductions can be characterized on a scale of increasing responsibility from natural expansion of species to direct human introduction. Here we examine three main categories: (1) natural range expansion, (2) climate change-driven range expansion, and (3) direct human introduction. These perceptions in turn will influence whether they are likely to support management programs to control a species. Individuals likely perceive the lowest responsibility for invasive species that naturally expand their ranges, and therefore we expect there to be the least support for eradication of naturally expanding species. Individuals may perceive greater

responsibility for invasive species that expand their ranges due to climate change. Finally, individuals are likely to perceive the greatest level of responsibility for invasive species introductions that result from intentional human-facilitated introductions; so, we expect there to be the greatest support for eradicating species that were put there by humans.

Environmentalism and attribution of responsibility

Level of environmental concern is likely to influence support for species eradication. The New Ecological Paradigm (NEP; Dunlap, Van Liere, Mertig, & Jones, 2000) is a scale to measure level of environmental concern. It has been shown to be a consistent predictor of environmental attitudes and behaviors of individuals in the US and abroad (Dunlap et al., 2000). Individuals who are higher on the NEP feel a stronger sense of urgency toward the environment, more concern for environmental risk, and are likely to be more supportive of policies that mitigate environmental problems (Dietz, Dan, & Shwom, 2007; Slimak & Dietz, 2006). For example, support for government initiatives to address air pollution is positively correlated with pro-environmental attitudes (Bord, O'Connor, & Fisher, 2000).

For species introductions, attribution of responsibility and level of environmental concern are likely to interact to produce support for or opposition to management policies. Level of environmental concern is positively correlated with perceptions of the risks associated with climate change (Carlton & Jacobson, 2013). This suggests that those who are low on the NEP perceive a lower level of risk associated with climate change. Therefore, people who have a low level of environmental concern are likely to have a lower level of concern for species introductions that are driven by climate change. Therefore, we predict that individuals who are low on the NEP scale will be more supportive of eradication policies when responsibility is attributed to human-mediated introduction, than when responsibility is attributed to climate change-mediated expansion.

In contrast to this, individuals who are high on the NEP scale likely perceive high risks to themselves and the environment from climate change, and when species introductions are attributed to climate change are likely to perceive a greater sense of urgency for mitigating the problem of species invasions than their lower NEP counterparts. They may perceive the impacts of climate change to be higher risk than the impacts of species that were intentionally introduced. Therefore, we predict that individuals who are high on the NEP scale will be more supportive of eradication policies when responsibility is attributed to climate change for species introductions, than when responsibility is attributed to human-mediated introduction.

Other factors influencing support

Awareness of species status

Knowledge and awareness about specific species can also influence support for environmental policies (Hiroyasu, Miljanich, & Anderson, 2019). People generally have low knowledge and awareness about both specific wildlife and wildlife policies (Kellert, 1984). We expect that people with low awareness about a species presence will likely be less supportive of management.

Concern for animal welfare

Concern for the rights and welfare of animal species is one reason for opposition to proposed eradication programs, and has been shown to be a significant predictor of support for interventions (DeGolia et al., 2019). People who have a higher level of concern for animal welfare are likely to be less supportive of species eradications.

Case Study: Wild Pigs

Here we test how different levels of attributed responsibility influence public support for invasive species eradication for the wild pigs (*Sus scrofa*) in California. And, we further examine

how this interacts with level of environmental concern. Wild pigs were established in California through multiple releases beginning in the 1500's and are widely distributed across the state (Sweitzer & McCann, 2007). They negatively impact wildlife and native plants through their foraging habits (Barrios-Garcia & Ballari, 2012; Bowman & McDonough, 1991; McClure, Burdett, Farnsworth, Sweeney, & Miller, 2018; Siemann, Carrillo, Gabler, Zipp, & Rogers, 2009). They are also known to impair water quality, be vectors of disease, cause crop and forage loss, and prey directly on livestock species (Barrios-Garcia & Ballari, 2012; Bevins, Pedersen, Lutman, Gidlewski, & Deliberto, 2014; Pech & Hone, 1988; Seward, VerCauteren, Witmer, & Engeman, 2004). It is estimated that wild pigs cause about $1.5 billion in damage and the associated control costs across the US annually (Pimentel, 2007). In general, the public has low knowledge about the presence of wildlife (Kellert, 1984), and because of their long history in the state, we expect that the public will have low knowledge about how wild pigs were introduced. Wild pigs are a useful case to test the role of framing because previous efforts to locally eradicate populations resulted in mixed support from the public, including vocal opposition (Markarian, 2005).

Methods

Survey Design

Participants and data collection

2073 Participants were recruited from a panel of Californians provided by Qualtrics between December 13 and December 20, 2019 using quotas for household income, political party affiliation, and gender to help ensure a representative sample. The survey measured support for wild pig eradication, level of environmental concern, political ideology, demographic characteristics, and perceptions of controllability and responsibility of wild pig populations. Respondents were randomly assigned to read a description of a proposed invasive species

management project that involves population reduction of a species. They were told it was a real proposal to eradicate invasive wild pigs in the state, and that the California Department of Fish and Wildlife was asking for public opinion on the proposal. Respondents received one of three possible treatments, which occurred across a scale of attributed responsibility. Each treatment highlighted a different way that invasive wild pigs arrived in the state: (1) through direct release by humans, (2) by natural expansion from a neighboring state, or (3) due to climate change-driven expansion of the population from a neighboring state. The treatments and all other survey questions are available in Supplement 1.

Support for eradication

To measure support for the proposed eradication, individuals were asked whether they supported or opposed an eradication program and how strongly they supported or opposed it. This yielded a six-point scale from strongly oppose to strongly support.

Environmental Concern

Environmental concern was measured using the New Ecological Paradigm (NEP; Dunlap et al., 2000). Respondents were asked how much they agreed or disagreed with 15 different statements about the environment on a 1-7 Likert scale. Negative questions were reverse coded, and the mean score was used as a measure of level of environmental concern. We treated NEP as a continuous variable and interacted it with the scale of attributed responsibility.

Awareness of species invasive status

Previous studies have found that general knowledge and awareness of wildlife in the American public is generally low (Kellert, 1984). To measure awareness of invasive species as a category of species, respondents were asked to identify six different species as invasive, native, or indicate if they did not know.

Concern for animal welfare

Respondents were asked how much they agreed or disagreed on a 5-point Likert scale with six statements about the welfare of animals. The mean of all six questions was taken as an overall score of concern for animal welfare. Individuals in the top quartile of scores were considered to have high concern for animal welfare.

Political ideology and demographic measures

Political ideology was self-reported by respondents who could select how liberal or conservative they were on a 7-point scale from very conservative to very liberal. Individuals self-reported their gender identity, age, and household income.

Statistical Analysis:

A linear model (OLS) was specified to examine the correlates of support for wild pig eradication. The dependent variable in all models was support for wild pig eradication. We conducted balance checks using chi-squared tests on gender, urban or rural residence, ideology, and household income across treatments to ensure balance between each treatment. We used an ANOVA to test for balance of age across treatment groups.

Results

Survey

Table 1 provides descriptive statistics for demographics of respondents and California benchmarks from the 2016 US Census American Community Survey. The sample was representative on household income, gender, and political party affiliation. Chi-squared and t-tests confirmed balance across treatments on gender ($\chi^2 = 0.29, p = 0.86$), age ($F(2, 2070) = 1.26, p = 0.28$), urban residence ($\chi^2 = 1.58, p = 0.81$), ideology ($\chi^2 = 10.31, p = 0.59$), and household income ($\chi^2 = 8.96, p = 0.71$).

Support for eradication

Mean support for eradication across all respondents was 4.62 (sd = 1.46) on a 1-6 scale, with higher scores representing higher support. Mean support was 4.78 (sd = 1.45, N = 716) for treatments that specified that humans introduced wild pigs, 4.65 (sd = 1.40, N = 666) for treatments that specified that wild pig populations naturally expanded into California, and 4.42 (sd = 1.51, N = 691) for treatments that specified that wild pig expansion was driven by climate change. Support was not significantly different between the human introduced and natural expansion treatment ($t = 2.99$, $p = 0.11$), but support for the human expansion treatment was significantly higher than support for the climate change-driven expansion treatment ($t = 4.54$, $p < 0.01$). Mean support for the natural expansion treatment was also significantly higher than the mean support for the climate change-driven treatment ($t = 2.99$, $p = 0.003$).

New Ecological Paradigm

Respondents had a mean score of 3.56 (median = 3.53, sd = 0.68; Supplemental Figure 1) on the New Ecological Paradigm scale. Those below the median score were considered non-environmentalists, while those above the median were considered environmentalists. Those in the

Interaction between attributed responsibility and level of ecological concern

Across the NEP scales, respondents were significantly less supportive of the treatment that specified climate change-driven expansion than the treatment that specified human introduction (Table 2). Support for eradication when populations naturally expanded into an area was indistinguishable from support for eradication policies when wild pigs were specified as being introduced by humans. To understand the role of responsibility we specified a model with

an interaction between treatment and NEP score. Figure 1 shows how the relationship between support and ecological concern differs between treatments across all NEP scores.

Using the NEP score, we divided the sample into environmentalists versus non-environmentalists and we found that there is no significant difference between support for eradication for environmentalists across treatments (Table 3) and individuals were not more supportive of eradication policies when frames attributed responsibility for species introductions to climate change-driven expansions than human-mediated introductions. For non-environmentalists, there is significantly lower support for eradicating an invasive species when the responsibility for the species presence is attributed to climate change (Table 4). There is also a positive and significant interaction between treatment and level of environmental concern. Overall, support for eradication of wild pig populations that were specified as having naturally expanded into the state is higher than support for populations that were attributed to climate change-driven expansion across all NEP scores except the highest (Table 2, NEP > 4.75).

Full Model

Model 2 expands on the previous model by including awareness of species invasive status and demographic covariates, including gender, level of urbanicity, household income, ideology, and education level (Table 5). Awareness of the invasive status of species is the strongest predictor of support for eradication, with a significant and positive relationship. Women are significantly less supportive of eradication policies than men, consistent with previous findings in the invasive species literature (Bremner and Park 2007; Fitzgerald et al. 2007). Both education and household income had small, but significantly positive relationships with support for eradication.

Subgroup analysis: High concern for animal welfare

To understand how support for eradication differed across treatments, we examined a subset of the data that scored the highest on our concern for animal welfare scale (Table 6; N = 672). This subgroup is likely to have the lowest support for eradication, so we expect there to be greater spread in the dependent variable than for the full sample where there is generally high support for eradication. Mean support for each treatment was 4.44 (sd =1.62) for the human introduced treatment, 4.27 (sd = 1.58) for the natural expansion treatment, and 4.10 (sd = 1.59) for the climate change-driven expansion treatment. Within the high concern for animal rights subgroup, there is no significant relationship between treatment type ($\beta_{\text{natural expansion}} = -0.41$, $p = 0.70$; $\beta_{\text{climate change}} = 0.03$, $p = 0.98$) or concern for the environment ($\beta_{\text{NEP}} = 0.14$, $p = 0.45$) and support for invasive species control.

Discussion

This work shows that across all surveyed individuals, there is the least support for eradication of invasive species when responsibility for the species introduction is attributed to climate change. Connecting species invasions to climate change is not compelling, even for those with high levels of environmental concern. And even for those who scored highest on the NEP, climate change frames never resulted in higher support than human introduction frames. This suggests that the general public may not connect climate change with the risks posed by species invasions or may not find climate change to be a compelling reason to manage invasive species. There may also be a mismatch in perceived temporal distance between invasive species and climate change, because the effects of climate change are often believed to be far away in both time and space. This expands on our understanding of how attributed responsibility is tied to motivating action to solve environmental problems.

Surprisingly, natural expansion treatments were indistinguishable from the human introduction frames. Unlike climate change (Spence et al., 2011) and pollution (Siegrist & Sütterlin, 2014), invasive species management does not fall into the category of environmental problems where the public is compelled to act when they believe they are directly responsible for the observed impacts. Respondents do not seem to differentiate between human caused introductions and naturally expanding populations of species, which may be a result of the strong impacts that invasive species can have on human livelihoods and impacts to ecosystem functions. Moreover, wild pigs and their associated impacts have recently "gone viral" across social media, so the public may be more informed about the origins of wild pigs. It is also possible that the broader public understands that humans are responsible for introducing wild pigs to neighboring areas, and thus saw all of our treatments as human introduction. Support for eradication of other introduced species that the public is less familiar with may differ across these treatments. This also suggests that the public is not more opposed to control of species that got to a place on their own, a concern that many managers may have.

In the full model, we found that awareness of invasive species status was an important predictor of support. People who were better at correctly identifying the invasive status of species in California were more supportive of eradication policies. This may be because they are more familiar with the consequences of invasive species. It also suggests that education programs identifying invasive species and their impacts may be compelling to the public. We also found that ideology was not a significant predictor of support for eradication, suggesting that invasive species are a non-politicized topic. However, Figure 2 shows that for the most conservative respondents, there is the least support for climate change treatments. This suggests that connecting invasive species to climate change would cause a loss in support when compared to highlighting when a species was introduced by humans. We conducted a subgroup analysis of

those with high concern for animal welfare and did not find differences between treatments. This suggests that level of responsibility cannot surpass respondents' concern for animal welfare.

Messages for Managers

There are multiple lessons for managers here. First, connecting climate change to species invasions is not compelling to the public. Concerns about the indirect consequences of climate change may be less tangible to the public, so highlighting the direct impacts of invasive species will be more effective (DeGolia et al., 2019). Further, the politicized nature of climate change and the results presented here suggest that connecting invasive species to climate change could cause more conservative members of the public to be less supportive of management programs. Second, distinguishing between naturally expanding populations and human-introduced invasions is not compelling to the public. Therefore managers need not spend limited time and resources highlighting the origin of the species they are trying to manage. Third, information campaigns that communicate which species are invasive and their associated impacts more broadly may help to increase support for management, as those who are more informed about which species are invasive are more supportive of controls. Fourth, ideology and concern for animal welfare did not change the patterns we see in support for eradication across treatments. This suggests that managers can have one broad message that appeals to the general public and messaging to specific subgroups is less important in information campaigns.

Across domains, emphasizing human responsibility for driving environmental problems is the most compelling to the California public. We show that linking environmental problems to climate change is not a compelling way to motivate the full public to support eradication programs. Managers can leverage this information to simplify their messaging to the broader public and thereby reduce opposition to eradication policies.

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References

Bandura, A. (1977). Self-efficacy: Toward a unifying theory of behavioral change. *Psychological Review*, *84*(2), 191–215. https://doi.org/10.1037/0033-295X.84.2.191

Barrios-Garcia, M. N., & Ballari, S. A. (2012). Impact of wild boar (Sus scrofa) in its introduced and native range: A review. *Biological Invasions*, *14*(11), 2283–2300. https://doi.org/10.1007/s10530-012-0229-6

Beierle, T. C. (1999). Using Social Goals to Evaluate Public Participation in Environmental Decisions. *Policy Studies Review*, *16*(3–4), 75–103. https://doi.org/10.1111/j.1541-1338.1999.tb00879.x

Bevins, S. N., Pedersen, K., Lutman, M. W., Gidlewski, T., & Deliberto, T. J. (2014). Consequences associated with the recent range expansion of nonnative feral swine. *BioScience*. https://doi.org/10.1093/biosci/biu015

Bichard, E., & Kazmierczak, A. (2012). Are homeowners willing to adapt to and mitigate the effects of climate change? *Climatic Change*, *112*(3–4), 633–654. https://doi.org/10.1007/s10584-011-0257-8

Böhm, G., & Pfister, H. R. (2000). Action tendencies and characteristics of environmental risks. *Acta Psychologica*, *104*(3), 317–337. https://doi.org/10.1016/S0001-6918(00)00035-4

Bord, R. J., O'Connor, R. E., & Fisher, A. (2000). In what sense does the public need to understand global climate change? *Public Understanding of Science*, *9*(3), 205–218. https://doi.org/10.1088/0963-6625/9/3/301

Bowman, D., & McDonough, L. (1991). Feral pig (Sus scrofa) rooting in a monsoon forest wetland transition, northern Australia. *Wildlife Research*, *18*(6), 761–765.

Bremner, A., & Park, K. (2007). Public attitudes to the management of invasive non-native species in Scotland. *Biological Conservation*, *139*(3–4), 306–314. https://doi.org/10.1016/J.BIOCON.2007.07.005

Butler, C., & Pidgeon, N. (2011). From "flood defence" to "flood risk management": Exploring governance, responsibility, and blame. *Environment and Planning C: Government and Policy*, *29*(3), 533–547. https://doi.org/10.1068/c09181j

Carlton, S. J., & Jacobson, S. K. (2013). Climate change and coastal environmental risk perceptions in Florida. *Journal of Environmental Management*, *130*, 32–39. https://doi.org/10.1016/j.jenvman.2013.08.038

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., … Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, *405*(6783), 234–242. https://doi.org/10.1038/35012241

Davis, J. J. (1995). The effects of message framing on response to environmental communications. *Journalism and Mass Communication Quarterly*, *72*, 285–299.

DeGolia, A. H., Hiroyasu, E. H. T., & Anderson, S. E. (2019). Economic losses or environmental gains? Framing effects on public support for environmental management. *PLoS ONE*, *14*(7), 1–17. https://doi.org/10.1371/journal.pone.0220320

Dietz, T., Dan, A., & Shwom, R. (2007). Support for climate change policy: social psychological and social structural influences. *Rural Sociology*, *72*(2), 185–214.

https://doi.org/10.1526/003601107781170026

Dunlap, R. E., Van Liere, K. D., Mertig, A. G., & Jones, R. E. (2000). New Trends in Measuring Environmental Attitudes: Measuring Endorsement of the New Ecological Paradigm: A Revised NEP Scale. *Journal of Social Issues*, *56*(3), 425–442. https://doi.org/10.1111/0022-4537.00176

Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., … Tatem, A. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, *7*, 12485. https://doi.org/10.1038/ncomms12485

Eden, S. (1996). Public participation in environmental policy: considering scientific, counter-scientific and non-scientific contributions. *Public Understand. Sci*, *5*, 183–204. https://doi.org/10.1088/0963-6625/5/3/001

Executive Order No. 13112, 58 Federal Register § (1993).

Ferguson, M. A., & Branscombe, N. R. (2010). Collective guilt mediates the effect of beliefs about global warming on willingness to engage in mitigation behavior. *Journal of Environmental Psychology*, *30*(2), 135–142. https://doi.org/10.1016/j.jenvp.2009.11.010

Hardisty, D. J., Johnson, E. J., & Weber, E. U. (2010). A dirty word or a dirty world? attribute framing, political affiliation, and query theory. *Psychological Science*, *21*(1), 86–92. https://doi.org/10.1177/0956797609355572

Hiroyasu, E. H. T., Miljanich, C. P., & Anderson, S. E. (2019). Drivers of support: The case of species reintroductions with an ill-informed public. *Human Dimensions of Wildlife*, *24*(5), 401–417. https://doi.org/10.1080/10871209.2019.1622055

Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., … Vilà, M. (2008). Grasping at the routes of biological invasions: a framework for integrating pathways into

policy. *Journal of Applied Ecology*, *45*(2), 403–414. https://doi.org/10.1111/j.1365-2664.2007.01442.x

Kaiser, F. G., Ranney, M., Hartig, T., & Bowler, P. A. (1999). Ecological Behavior, Environmental Attitude, and Feelings of Responsibility for the Environment. *European Psychologist*, *4*(2), 59–74. https://doi.org/10.1027//1016-9040.4.2.59

Kellert, S. R. (1984). American-Attitudes Toward and Knowledge of Animals: An Update. In M. W. Fox & L. D. Mickley (Eds.), *Advances in Animal Welfare Science* (pp. 177–213). Washington, DC: The Humane Society of the United States. https://doi.org/10.1007/978-94-009-4998-0_11

Lakoff, G. (2010). Why it Matters How We Frame the Environment. *Environmental Communication*, *4*(1), 70–81. https://doi.org/10.1080/17524030903529749

Levin, I. P., Schneider, S. L., & Gaeth, G. J. (1998). All Frames Are Not Created Equal: A Typology and Critical Analysis of Framing Effects. *Organizational Behavior and Human Decision Processes*, *76*(2), 149–188. https://doi.org/10.1006/obhd.1998.2804

Mack, M. C., & D'Antonio, C. M. (1998). Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, *13*(5), 195–198. https://doi.org/10.1016/S0169-5347(97)01286-X

Malka, A., Krosnick, J. A., & Langer, G. (2009). The association of knowledge with concern about global warming: Trusted information sources shape public thinking. *Risk Analysis*, *29*(5), 633–647. https://doi.org/10.1111/j.1539-6924.2009.01220.x

Markarian, M. (2005). Pig eradication plan out of control - SFGate. Retrieved December 4, 2019, from https://www.sfgate.com/green/article/Pig-eradication-plan-out-of-control-2668922.php

Markowitz, E. M., & Shariff, A. F. (2012). Climate change and moral judgement. *Nature Climate*

Change, *2*(4), 243–247. https://doi.org/10.1038/nclimate1378

McClure, M. L., Burdett, C. L., Farnsworth, M. L., Sweeney, S. J., & Miller, R. S. (2018). A globally-distributed alien invasive species poses risks to United States imperiled species. *Scientific Reports*, *8*(1), 5331. https://doi.org/10.1038/s41598-018-23657-z

McNeely, J. A. (2001). *The Great Reshuffling: Human dimensions of alien invasive species.*

Menéndez, R., González-Megías, A., Lewis, O. T., Shaw, M. R., & Thomas, C. D. (2008). Escape from natural enemies during climate-driven range expansion: A case study. *Ecological Entomology*, *33*(3), 413–421. https://doi.org/10.1111/j.1365-2311.2008.00985.x

Nisbet, M. C., Markowitz, E. M., & Kotcher, J. E. (2012). Winning the Conversation: Framing and Moral Messaging in Environmental Campaigns. *Talking Green: Exploring Current Issues in Environmental Communication*, 9–36.

Parmesan, C. (1996). Climate and species' range. *Nature*. https://doi.org/doi: 10.1038/382765a0

Pech, R. P., & Hone, J. (1988). A Model of the Dynamics and Control of an Outbreak of Foot and Mouth Disease in Feral Pigs in Australia. *Journal of Applied Ecology*, *25*(1), 63–77.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*. https://doi.org/10.1126/science.aai9214

Pimentel, D. (2007). Environmental and Economic Costs of Vertebrate Species Invasions Into the United States. In *Managing Vertebrate Invasive Species* (pp. 1–8). USDA National Wildlife Research Center.

Pimentel, D., Lach, L., Zuniga, R., & Morrison, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience*, *50*(1), 53–65. https://doi.org/10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic

costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3 SPEC. ISS.), 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine taxa track local climate velocities. *Science*, *341*(6151), 1239–1242. https://doi.org/10.1126/science.1239352

Seward, N. W., VerCauteren, K. C., Witmer, G. W., & Engeman, R. M. (2004). Feral swine impacts on agriculture and the environment. *Sheep and Goat Research Journal*, *19*(October), 34–40. Retrieved from http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1011&context=icwdmsheepgoat

Siegrist, M., & Sütterlin, B. (2014). Human and nature-caused hazards: the affect heuristic causes biased decisions. *Risk Analysis : An Official Publication of the Society for Risk Analysis*, *34*(8), 1482–1494. https://doi.org/10.1111/risa.12179

Siemann, E., Carrillo, J. a, Gabler, C. a, Zipp, R., & Rogers, W. E. (2009). Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. *Forest Ecology and Management*, *258*(5), 546–553. https://doi.org/10.1016/j.foreco.2009.03.056

Simberloff, D. A., Parker, I. M. B., & Windle, P. N. C. (2005). Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment*, *3*(1 SPEC. ISS.), 12–20. https://doi.org/10.1890/1540-9295(2005)003[0012:ISPMAF]2.0.CO;2

Simberloff, D. S., Parker, I. M., & Windle, P. N. (2005). Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment*, *3*(1 SPEC. ISS.), 12–20. https://doi.org/10.1890/1540-9295(2005)003[0012:ISPMAF]2.0.CO;2

Slimak, M. W., & Dietz, T. (2006). Personal values, beliefs, and ecological risk perception. *Risk Analysis*, *26*(6), 1689–1705. https://doi.org/10.1111/j.1539-6924.2006.00832.x

Spence, A., Poortinga, W., Butler, C., & Pidgeon, N. F. (2011). Perceptions of climate change and willingness to save energy related to flood experience. *Nature Climate Change*, *1*(1), 46–49. https://doi.org/10.1038/nclimate1059

Sweitzer, R. A., & McCann, B. E. (2007). *Natural areas ecological damage and economic costs survey report*. Retrieved from http://www.sdmmp.com/Libraries/Management_Plans_and_Reports/PIGS_Natural_Area_Survey_Report.sflb.ashx

United Nations. Convention on Biological Diversity (1992). https://doi.org/10.1146/annurev.ento.48.091801.112645

Weiner, B. (1993). On sin versus sickness: A theory of perceived responsibility and social motivation. *American Psychologist*, *48*(9), 957–965. https://doi.org/10.1037/0003-066X.48.9.957

Figures

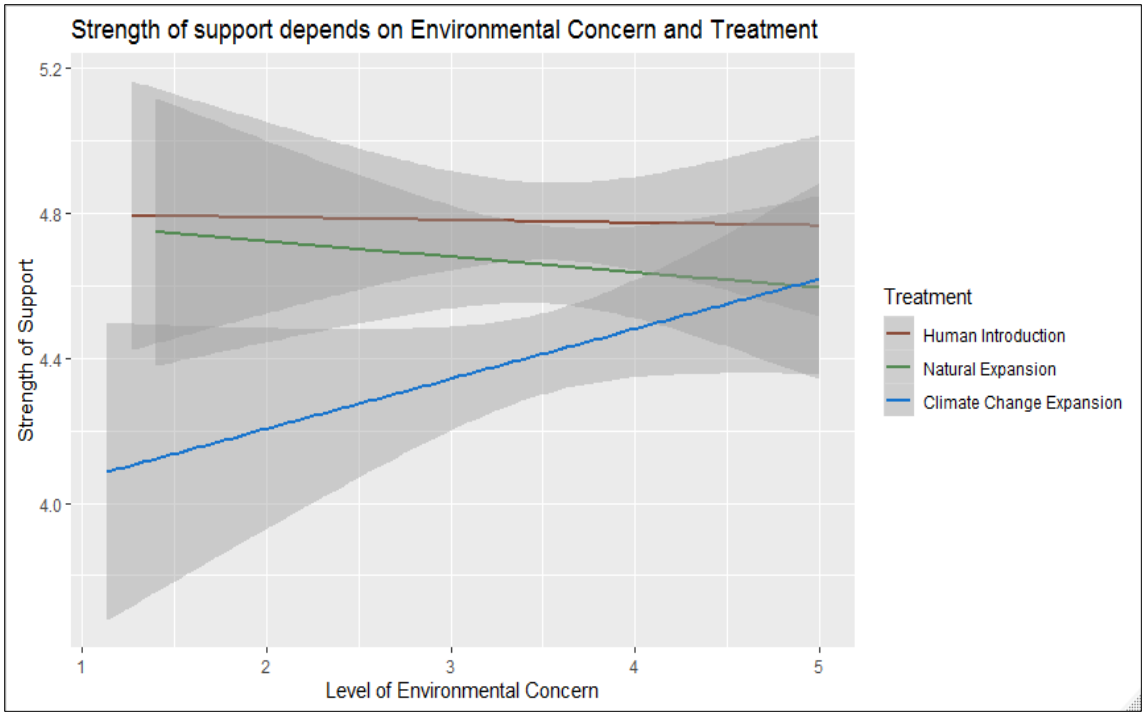


Figure 1: Strength of support for invasive species eradication (scored on a 1-6 scale) by level of environmental concern (NEP), which is a mean score for individual respondents. Each line represents a different treatment.

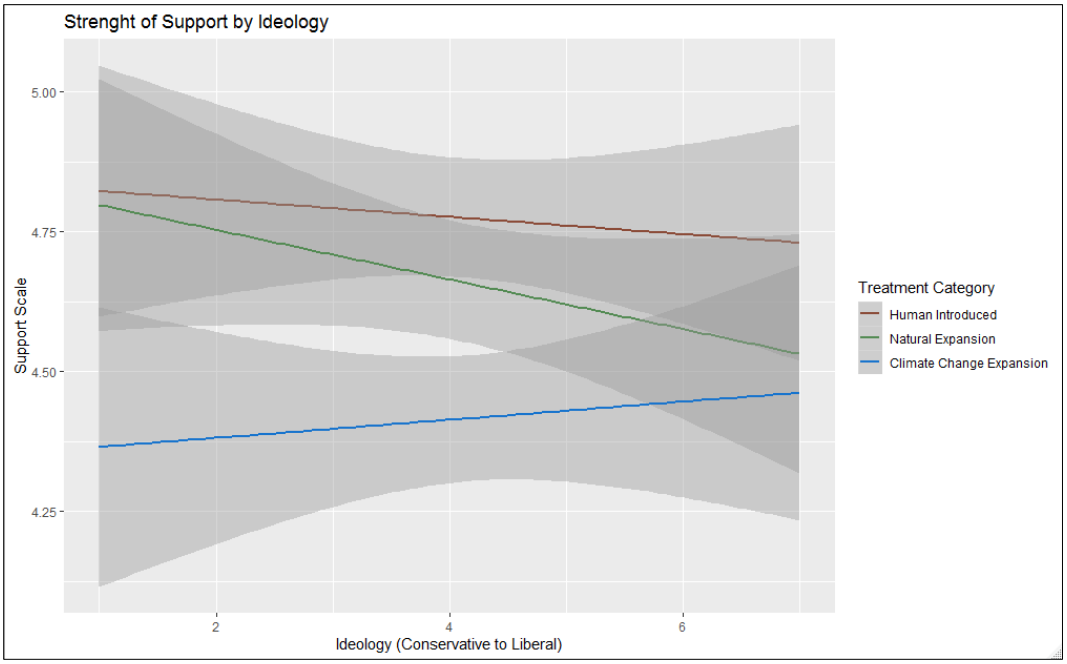


Figure 2: Strength of support for invasive species eradication (scored on a 1-6 scale) by ideology (1-7 scale), where conservatives are at the low end of the scale and liberals are at the higher end of the scale. Each line represents a different treatment.

Tables

Table 1: Summary statistics of sample population compared to California averages.

Variable	Sample Statistics	California
Age		
18-25 yrs	8.0% (165)	7.5%
26-35 yrs	9.7% (201)	14.2%
36-50 yrs	11.1% (231)	20.1%
51-65 yrs	25.3% (524)	18.5%
>65 yrs	45.9% (952)	12.9%
Gender		
Male	48.2% (1001)	49.0%
Female	51.7% (1072)	51.0%
Household Income		
<$40,000	38% (786)	25.4%
$40,000-65,000	19% (392)	26.8%
$65,000-100,000	13% (273)	28.5%
$100,00-250,000	24% (506)	8.3%
>$250,000	3% (66)	11.0%
Education		
HS Grad or Less	16% (322)	37.6%
Some College	34% (709)	29.1%
Bachelor's Degree	31% (639)	20.8%
Advanced Degree	19% (401)	12.5%
Total Bachelors or Higher	50% (1040)	33.3%
Race		
Non-Hispanic White	77% (1593)	38%
Hispanic	6% (118)	39%
Asian	9% (188)	14%
Black	5% (101)	6%
American Indian	1% (28)	<1%
Household Location		
Rural	32% (279)	13%
Urban/Suburban	68% (1788)	87%
Party ID		
Democrat	39% (799)	44.8%
Republican	28% (574)	27.3%
Independent	30% (632)	23.3%

Note: California demographic statistics taken from 2016 US Census American Community Survey. California ages do not sum to 100% because the census includes a breakdown of ages for people under 18 years of age. The measure of household income is ordinal, with each level corresponding to an income bracket, rather than a specific amount, and income brackets used in the US Census do not overlap with ours. Party identification information taken from the Public Policy Institute of California's January 2019 survey of Californians. CA population data for age are estimates, as age bins do

not align between the ACS and our survey. Sample size is in parentheses following the sample statistic.

Table 2: Model 1 summary statistics of the relationship between support for invasive species eradication and level of environmental concern for different treatment groups. Standard errors are presented in parentheses below the coefficient.

Model 1 Summary

	Dependent variable:
	Support Scale
Natural Expansion	0.005
	(0.426)
Climate Change-Driven Expansion	-0.873**
	(0.410)
NEP (continuous)	-0.008
	(0.080)
Natural Expansion:NEP	-0.035
	(0.117)
Climate Change-Driven Expansion:NEP	0.145
	(0.113)
Constant	4.803***
	(0.288)
Observations	2,073
Log Likelihood	-3,715.504
Akaike Inf. Crit.	7,443.007
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 3: Summary statistics of the relationship between support and NEP for environmentalists. Here non-environmentalists are described as people who had an NEP score less than 4.33. Standard errors are presented in parentheses below the coefficient.

Summary of Support for Eradication for Environmentalists

	Dependent variable:
	SupportScale
Natural Expansion	-0.205
	(1.158)
Climate Change-Driven Expansion	1.285
	(1.135)
NEP	0.084
	(0.198)
Natural Expansion:NEP	0.011
	(0.284)
Climate Change-Driven Expansion:NEP	-0.391
	(0.278)
Constant	4.468***
	(0.808)
Observations	1,112
Log Likelihood	-1,993.611
Akaike Inf. Crit.	3,999.222
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 4: Summary statistics of the relationship between support and NEP for non-environmentalists. Here non-environmentalists are described as people who had an NEP score less than 4.33. Standard errors are presented in parentheses below the coefficient.

Summary of Support for Eradication for Non-Environmentalists

	Dependent variable:
	SupportScale
Natural Expansion	-0.400
	(0.827)
Climate Change-Driven Expansion	-2.905***
	(0.802)
NEP	-0.392**
	(0.193)
Natural Expansion:NEP	0.115
	(0.275)
Climate Change-Driven Expansion:NEP	0.841***
	(0.268)
Constant	5.894***
	(0.575)
Observations	961
Log Likelihood	-1,715.442
Akaike Inf. Crit.	3,442.885
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 5: Full model summary statistics of the relationship between support for invasive species eradication and level of environmental concern for different treatment groups, gender, urbanicity, household income, ideology, education, and awareness of species invasive status. Standard errors are presented in parentheses below the coefficient.

Full Model Summary

	Dependent variable:
	SupportScale
Natural Expansion	0.015
	(0.406)
Climate Change-Driven Expansion	-0.868**
	(0.393)
NEP	-0.088
	(0.080)
Female	-0.327***
	(0.063)
Suburban	-0.103
	(0.069)
Rural	-0.056
	(0.100)
Household Income	0.033
	(0.022)
Ideology	0.0003
	(0.021)
Education	0.048
	(0.035)
Awareness of Invasive Status	1.692***
	(0.138)
Natural Expansion:NEP	-0.034
	(0.112)
Climate Change-Driven Expansion:NEP	0.151
	(0.109)
Constant	4.001***
	(0.332)
Observations	2,061
Log Likelihood	-3,579.204

Akaike Inf. Crit.	7,184.407
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 6: Model 3 summary statistics of the relationship between support for invasive species eradication and level of environmental concern for different treatment groups for respondents with high concern for animal welfare. Standard errors are presented in parentheses below the coefficient.

High Concern for Animal Welfare Model Summary

	Dependent variable:
	Support
Natural Expansion	-0.410
	(1.073)
Climate Change-Driven Expansion	0.027
	(0.999)
NEP	0.138
	(0.181)
Natural Expansion:NEP	0.062
	(0.271)
Climate Change Driven-Expansion:NEP	-0.092
	(0.252)
Constant	3.899***
	(0.717)
Observations	672
Log Likelihood	-1,265.913
Akaike Inf. Crit.	2,543.825
Note:	*p<0.1; **p<0.05; ***p<0.01

Supplemental Information:

Survey Questions

New Environmental Paradigm Questions

Please read each of the following statements and indicate whether you strongly agree, mostly agree, are unsure, mostly disagree, or strongly disagree. There are no right or wrong answers.

	Strongly agree (1)	Somewhat agree (2)	Neither agree nor disagree (3)	Somewhat disagree (4)	Strongly disagree (5)
We are approaching the limit of the number of people the earth can support.	○	○	○	○	○
Humans have the right to modify the natural environment to suit their needs.	○	○	○	○	○
When humans interfere with nature it often produces disastrous consequences.	○	○	○	○	○
Human ingenuity will ensure that we do NOT make the earth unlivable.	○	○	○	○	○
Humans are severely abusing the environment.	○	○	○	○	○
The earth has plenty of natural resources if we just learn to develop them.	○	○	○	○	○
Plants and animals have as much right as humans to exist.	○	○	○	○	○
The balance of nature is strong enough to cope with the impacts of modern industrial nations.	○	○	○	○	○
Despite our special abilities humans are still subject to the laws of nature.	○	○	○	○	○
The so-called "ecological crisis" facing humankind has been greatly exaggerated.	○	○	○	○	○
The earth is like a spaceship with very limited room and resources.	○	○	○	○	○
Humans were meant to rule over the rest of nature.	○	○	○	○	○

The balance of nature is very delicate and easily upset.	○	○	○	○	○
Humans will eventually learn enough about how nature works to be able to control it.	○	○	○	○	○
If things continue on their present course, we will soon experience a major ecological catastrophe.	○	○	○	○	○

As a California resident, would you say that you support or oppose the wild pig management project you just read about?

- ○ Support (1)
- ○ Oppose (2)

How strong is your opposition to the project? Would you say that you strongly oppose, oppose, or only slightly oppose it?

- ○ Strongly Oppose (1)
- ○ Oppose (2)
- ○ Only slightly oppose (3)

How strong is your support for the project? Would you say that you strongly support, support, or only slightly support it?

- ○ Strongly Support (1)
- ○ Support (2)
- ○ Only slightly support (3)

Indicate whether you think each of the following species are invasive or native to California.

	Invasive	Native	Don't Know
Wild Pigs	○	○	○
Coyotes	○	○	○
Mountain Lions	○	○	○
Nutria	○	○	○
Black Bears	○	○	○
Grass carp fish	○	○	○

Wild pigs entered California by...

- ○ Intentional human introduction (1)
- ○ Natural expansion of populations (2)
- ○ Climate change-driven expansion (3)

Controllability How much control do you think humans have over nature?

- ○ A great deal (1)
- ○ A lot (2)
- ○ A moderate amount (3)
- ○ A little (4)
- ○ None at all (5)

How responsible are humans for the presence of wild pigs in California?

- ○ Humans are entirely responsible for wild pig presence. (1)
- ○ Humans have some responsibility for wild pig presence. (2)
- ○ Humans have no responsibility for wild pig presence. (3)

Please indicate whether you strongly agree, somewhat agree, neither agree nor disagree, somewhat disagree, or strongly disagree with the following statements. There is no right answer.

	Strongly agree (1)	Somewhat agree (2)	Neither agree nor disagree (3)	Somewhat disagree (4)	Strongly disagree (5)
I am very concerned about pain and suffering of animals.	○	○	○	○	○
I have seriously considered becoming a vegetarian in an effort to save animal lives.	○	○	○	○	○
Humans have no right to displace wild animals by converting wilderness areas into farmlands, cities, and other things designed for people.	○	○	○	○	○
Animals were put onto earth for humans to use.	○	○	○	○	○
The needs of people are always more important than the rights of animals.	○	○	○	○	○
The rights of people and the rights of animals are equally important.	○	○	○	○	○

As compared with the economy, how important is a political candidate's stance on ENVIRONMENTAL ISSUES when you are deciding who to vote for?

- ○ Extremely important (1)
- ○ Very important (2)
- ○ Moderately important (3)
- ○ Slightly important (4)
- ○ Not at all important (5)

As compared with the economy, how important is a political candidate's stance on IMMIGRATION ISSUES when you are deciding who to vote for?

- ○ Extremely important (1)
- ○ Very important (2)
- ○ Moderately important (3)
- ○ Slightly important (4)
- ○ Not at all important (5)

When asking people about elections, we often find that a lot of people were not able to vote because they weren't registered, they were sick, or they just didn't have time. Which of the following statements best describes you?

- ○ Did not vote in the presidential election in 2016. (1)
- ○ Thought about voting in the presidential election, but didn't. (2)
- ○ I usually vote, but didn't this time (3)
- ○ I am sure I voted in the 2016 presidential election. (4)

In general, how interested are you in politics and public affairs?

- ○ Extremely Interested (1)
- ○ Interested (2)
- ○ Somewhat interested (3)
- ○ Neither interested nor uninterested (4)
- ○ Somewhat uninterested (5)
- ○ Uninterested (6)
- ○ Extremely Uninterested (7)

Generally speaking, do you consider yourself a Republican, a Democrat, an Independent, or other?

- ○ Republican (1)
- ○ Democrat (2)
- ○ Independent (3)
- ○ Other, please specify (4) _____

Do you think of yourself as closer to the Republican Party or to the Democratic party?

- ○ Closer to the Republican Party (1)
- ○ Closer to the Democratic Party (2)

If Democrat: Would you consider yourself a strong Democrat or a not very strong Democrat?

- ○ Strong Democrat (1)
- ○ Not very strong Democrat (2)

If Republican: Would you consider yourself a strong Republican or a not very strong Republican?

- ○ Strong Republican (1)
- ○ Not very strong Republican (2)

Where would you place yourself on this scale?

- ○ Extremely liberal (1)
- ○ Liberal (2)
- ○ Somewhat liberal (3)
- ○ Moderate, middle of the road (4)
- ○ Somewhat conservative (5)
- ○ Conservative (6)
- ○ Extremely conservative (7)

How old are you?

What is your gender identity?

- ○ Man (1)
- ○ Woman (2)
- ○ Other (specify) (3) _____

What is your main occupation? (If retired, please state what your primary occupation was while working)

- ○ Management, professional, and related (1)
- ○ Service industry (2)
- ○ Sales (3)
- ○ Farming, fishing, or forestry (4)

- ○ Construction, extraction, or maintenance (5)
- ○ Production, transportation, or material moving (6)
- ○ Government (7)
- ○ Education (9)
- ○ Unemployed (8)

Which of the following best describes the area where you currently live.

- ○ Urban Community (1)
- ○ Suburban Community (2)
- ○ Rural Community (3)

Please enter your current zip code.

Choose one or more races that you consider yourself to be.

- ☐ White (1)
- ☐ Black or African American (2)
- ☐ American Indian or Alaska Native (3)
- ☐ Asian (4)
- ☐ Native Hawaiian or Pacific Islander (5)
- ☐ Other (6) _____

Are you Hispanic, Latino or Spanish, or none of these?

- ○ Yes (1)
- ○ None of these (2)

What is the highest level of formal education you have attained?

- ○ Primary school and/or some high school (1)
- ○ High school graduate (or equivalent) (2)
- ○ Some college or Associate's degree (3)
- ○ Bachelor's degree (4)
- ○ Advanced degree (e.g. Ph.D., J.D., M.D.) (5)

What is your current total household income in US dollars?

- ○ Less than $20,000 (1)
- ○ $20,000 - $39,999 (2)
- ○ $40,000 - $64, 999 (3)
- ○ $65,000 - $99,999 (4)
- ○ $100,000 - $250,000 (5)
- ○ More than $250,000 (6)
- ○ Rather not say (7)

Treatment Messages:

Human-mediated invasion

Program to Eliminate Invasive Pigs in California

For Immediate Release

December 1, 2019

California Department of Fish and Wildlife

The California Department of Fish and Wildlife (CDFW) confirmed the presence of invasive wild pigs in the state as a result of human release. Wild pigs are a prolific pest species that cause a variety of problems across the areas that they invade.

Using DNA analysis, CDFW scientists have confirmed that individuals were intentionally released by a recently closed agricultural operation. Both males and females were released, including pregnant females who have successfully reared multiple litters of wild pigs. Once released into the wild, pigs become feral quickly and wreak havoc on the communities they invade. There are few predators of wild pigs, so their populations have been able to grow quickly.

Intentionally introduced wild pigs are known to damage the ecosystem in a variety of ways. They damage riverbanks and fragile natural communities of plants and animals like oak woodlands and forest communities. They also often use agricultural areas for habitat and feed on agricultural crops, causing losses to farmers or reducing forage quality for livestock producers. Finally, wild pigs also spread diseases and parasites that can be transmitted to livestock or other work animals such as horses or cattle, including brucellosis, septicemia, and tapeworms.

The intentionally introduced wild pigs pose threats to California's native ecosystems and economy. Control measures for wild pigs have been activated, and CDFW is proposing a rigorous approach to address the problem.

The proposal involves a program to trap and kill wild pig populations in every county of the state where they are currently present. Ultimately, the CDFW has the goal of eliminating the entire population across the state.

CDFW is asking the public for their input and support on the project before planned early-stage implementation in early 2020.

Natural expansion

Program to Eliminate Invasive Pigs in California

For Immediate Release

December 1, 2019

California Department of Fish and Wildlife

The California Department of Fish and Wildlife (CDFW) confirmed the presence of invasive wild pigs in the state as a result of human release. Wild pigs are a prolific pest species that cause a variety of problems across the areas that they invade.

Using DNA analysis, CDFW scientists have confirmed that the population has expanded from a population in southern Oregon. Wild pigs are territorial and both males and females have dispersed from large populations in southern Oregon into California. The Oregon population of wild pigs is prolific and large groups have been observed in many areas of northern California. Wild pigs are able to reproduce quickly and there are few predators of wild pigs, allowing for rapid southward expansion into California.

Naturally expanding populations of wild pigs are known to damage the ecosystem in a variety of ways. They damage riverbanks and fragile natural communities of plants and animals like oak woodlands and forest communities. They also often use agricultural areas for habitat and feed on agricultural crops, causing losses to farmers or reducing forage quality for livestock producers. Finally, wild pigs also spread diseases and parasites that can be transmitted to livestock or other work animals such as horses or cattle, including brucellosis, septicemia, and tapeworms.

The naturally expanding populations of wild pigs pose threats to California's native ecosystems and economy. Control measures for wild pigs have been activated, and CDFW is proposing a rigorous approach to address the problem.

The proposal involves a program to trap and kill wild pig populations in every county of the state where they are currently present. Ultimately, the CDFW has the goal of eliminating the entire population across the state.

CDFW is asking the public for their input and support on the project before planned early-stage implementation in early 2020.

Climate driven invasion

Program to Eliminate Invasive Pigs in California

For Immediate Release

December 1, 2019

California Department of Fish and Wildlife

The California Department of Fish and Wildlife (CDFW) confirmed the presence of invasive wild pigs in the state as a result of human release. Wild pigs are a prolific pest species that cause a variety of problems across the areas that they invade.

Using long term monitoring data of the species, CDFW scientist have confirmed that wild pig population expansion has been driven by climate change. Climate change is increasing temperatures, making winters more mild, thus allowing wild pigs to expand their range northward across the state. Climate change-driven movements mean that wild pigs are now able to access many areas and habitats in the state that were previously unlivable for the species. Wild pigs are able to reproduce quickly and there are few predators of wild pigs, allowing for rapid northward expansion into California.

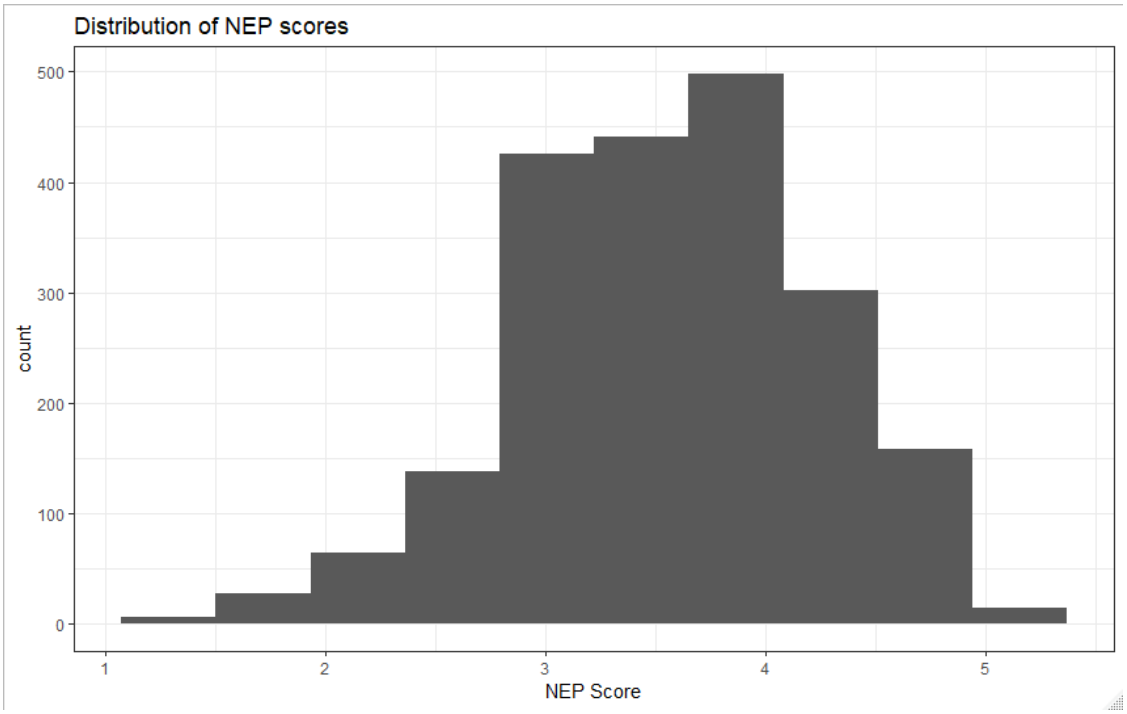
Climate change-driven populations of wild pigs are known to damage the ecosystem in a variety of ways. They damage riverbanks and fragile natural communities of plants and animals like oak woodlands and forest communities. They also often use agricultural areas for habitat and feed on agricultural crops, causing losses to farmers or reducing forage quality for livestock producers. Finally, wild pigs also spread diseases and parasites that can be transmitted to livestock or other work animals such as horses or cattle, including brucellosis, septicemia, and tapeworms.

The climate change-driven populations of wild pigs pose threats to California's native ecosystems and economy. Control measures for wild pigs have been activated, and CDFW is proposing a rigorous approach to address the problem.

The proposal involves a program to trap and kill wild pig populations in every county of the state where they are currently present. Ultimately, the CDFW has the goal of eliminating the entire population across the state.

CDFW is asking the public for their input and support on the project before planned early-stage implementation in early 2020.

Supplemental Figures:



Distrbution of NEP scores across all respondents. Median score was 3.53 and the mean score was 3.56.

CHAPTER IV:

DRIVERS OF SUPPORT: THE CASE OF SPECIES REINTRODUCTIONS WITH AN ILL-INFORMED PUBLIC

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Abstract

Successful rewilding of large carnivores depends on public acceptance, but the public frequently has little awareness about wildlife and specific reintroduction proposals. This article evaluated the determinants of public support for grizzly bear reintroduction in California to understand how value orientations, political ideology, and demographics predict attitudes when the public has little species-specific knowledge. We surveyed 980 Californians, showing that value orientations, awareness, and perceptions of costs and benefits shaped attitudes toward grizzly reintroduction, even when only one-quarter of the respondents knew that grizzly bears were extirpated from California. Almost two-thirds of respondents were supportive of reintroduction, rationalizing their support with assessments of societal and ecological costs and benefits. Lack of public awareness, perceptions of personal threats, and willingness to rationalize stated preferences provide cautionary notes to managers. Our results suggest that managers should offer early articulation of costs, benefits, and threats before reintroductions become politicized and opposition becomes entrenched.

Introduction

In areas from nanotechnology (Scheufele & Lewenstein, 2005) to nuclear energy (Stoutenborough, Sturgess, & Vedlitz, 2013), people form opinions regarding policies about which they have very little knowledge. Because policymakers are often responsive to public opinion, this can influence whether a policy is successful (Daniels, Krosnick, Tichy, & Tompson, 2012). Wildlife policies are no exception: people have little knowledge and awareness about wildlife (Kellert, 1984; Wilson & Tisdell, 2005) and public opinion can stop or stall management (e.g., Selge, Fischer, & van der Wal, 2011). This article used the case of grizzly bear (*Ursus arctos*) reintroduction as an example of a low knowledge environment to examine predictors of attitudes toward policy. Understanding the correlates of attitudes prior to a specific proposal can allow managers to predict where reintroduction may be supported versus problematic and inform how they engage with the community to build support for reintroductions.

The Cognitive Hierarchy, Value Orientations, and Policy Attitudes

The cognitive hierarchy has been used to understand how social cognitions from abstract values to value orientations to specific attitudes and beliefs influence behaviors (Fulton, Manfredo, & Lipscomb, 1996; Whittaker, Vaske, & Manfredo, 2006). Values occur at the bottom of the cognitive hierarchy (Fulton et al., 1996). They define what is important to us, how we think about ourselves, and how we fit into broader society (Allport, 1961; Bardi & Schwartz, 2003; Rokeach, 1973). They shape the goals and motivations that influence people's behavior (Schwartz, 2010) and are characterized as being deeply held, abstract, and changing little over a person's lifetime (Roccas, Sagiv, Schwartz, & Knafo, 2002; Rokeach, 1973; Schwartz & Bardi, 1997). Values have broad empirical support as predictors of policy attitudes (Schwartz, 2010; Schwartz, Caprara, & Vecchione, 2010) and can be measured consistently across people and even nations (de Groot & Steg, 2007; Schwartz, 2003; Schwartz, Lehmann, & Roccas, 1999).

Value orientations are patterns of beliefs about general objects, like the environment, that help link abstract values to attitudes, norms, and behaviors (Fulton et al., 1996; Vaske & Donnelly, 1999; Vaske, Donnelly, Williams, & Jonker, 2001). While previous research has considered value orientations specific to wildlife (Fulton et al., 1996; Kellert, 1984, 1994), we integrated the study of wildlife with broader characterizations of environmental value orientations (Kusmanoff et al., 2016; Schwartz, 2003; Schwartz et al., 1999). Environmental value orientations are similar to the "protection-use" wildlife value orientation continuum and can be characterized on a spectrum from anthropocentric to biocentric (Gagnon Thompson & Barton, 1994; Vaske & Donnelly, 1999; Whittaker et al., 2006). Three value orientations have been shown to be associated with attitudes toward environmental issues more generally: egoism, altruism, and biospherism (de Groot & Steg, 2007; Kusmanoff et al., 2016; Stern & Dietz, 1994; Vaske et al., 2001). Egoism is a person's concern for self (which is anthropocentric), altruism is a person's anthropocentric concern for others, and biospherism is a person's concern for non-human species. Altrusim and biospherism often predict support for environmental policies, whereas egoism typically predicts opposition to environmental policies (Schwartz, 2003; Schwartz et al., 1999).

Attitudes describe how individuals feel about specific issues and are influenced by value orientations and other factors. They are formed when a person evaluates an object, such as the reintroduction of grizzly bears. General environmental value orientations, like the ones measured here, predict general attitudes toward environmental actions better than specific attitudes (Whittaker et al., 2006). However, evaluating how general value orientations relate to specific attitudes toward reintroductions contributes to broader theory of natural resource decision making and a more specific understanding of attitudes and behaviors toward wildlife.

Factors outside the cognitive hierarchy are also likely to influence attitudes. People may rely on cues from political elites to determine their support for a policy (Gilens & Murakawa, 2002; Sniderman, Brody, & Tetlock, 1991). Liberals are generally more supportive of pro-environmental policies, including wildlife policies, than conservatives (Daniels et al., 2012). Demographic characteristics are also likely to be important predictors of attitudes toward policy. For example, age, race, education, and income are important predictors of support for climate change policies (Dietz, Dan, & Shwom, 2007; Holian & Kahn, 2015). Urban voters are generally more supportive of environmental initiatives than their non-urban counterparts (Bath, 1989; Williams, Ericsson, & Heberlein, 2002). Perceptions of societal costs and benefits and evaluations of personal threats may also shape attitudes toward policy. For example, perceived benefits and costs influence activism around air pollution policies (Lubell & Vedlitz, 2006).

Policy Support Predictors in Environments with Low Species-Specific Knowledge

Knowledge and awareness about specific policies can shape how people form attitudes. The public knowledge environments surrounding policy can be characterized on a continuum from general awareness to detailed and specific knowledge (Trevethan, 2017). Wildlife policy and management generally occur in a low knowledge environment where people have particularly low awareness of wildlife (Kellert, 1984). For example, a study in the UK found people were interested in marine environmental issues, but awareness about specific issues was low because of limited availability of information (Fletcher, Potts, Heeps, & Pike, 2009). In the Southwest US, awareness of mountain lion presence and impacts is very low even in places bordering where mountain lions are common (Casey, Krausman, Shaw, & Shaw, 2005). Policies to reintroduce species are becoming increasingly common, but there is a general lack of knowledge about wildlife, reintroductions, and their consequences (Reading, Clark, & Kellert, 1991).

Increasing awareness can shape support for a management practice. For example, as people have learned more about prescribed fires, they have become more supportive of prescribed burn policies (Loomis, Bair, & Gonzalez-Caban, 2001) and more knowledge about manatees is associated with greater support for conservation measures (Aipanjiguly, Jacobson, & Flamm, 2003). Awareness of an issue shapes the way people form their attitudes, but the way this information is taken in and synthesized into an attitude is influenced by both abstract value orientations, political orientations, social norms, and other factors (Fishbein & Ajzen, 1975; Zelezny, 1999). When awareness is low, individuals may not know what the more specific norms are, so value orientations may predict their attitude toward a wildlife issue. We assessed whether value orientations, political ideology, and demographics can predict policy attitudes prior to broad public awareness of the issue.

Case Study: Reintroduction of Grizzly Bears to California

The possible reintroduction of the grizzly bear to California provides a useful case study for assessing whether typical predictors of support for policy, such as value orientations, political ideology, and demographics, can be used to predict public attitudes prior to broad public awareness of any reintroduction proposal. Despite its extirpation in the 1920s, the California grizzly is still an important cultural symbol that is recognizable to the California public in images from the state flag to university mascots. In 2014, the Center for Biodiversity (CBD) petitioned the United States Fish and Wildlife Service (USFWS) to list California as part of the native range of grizzlies, thereby extending the range of possible recovery areas (Center for Biological Diversity, 2014). However, the USFWS rejected this petition and there are currently no plans to reintroduce the grizzly to California. Given that the species is absent from the state and the CBD petition was rejected, we hypothesize that awareness of grizzly bears in California is low.

As a result, we expect that the public's attitudes will be influenced by more general factors such as value orientations, political ideology, and demographics. This makes grizzly bear reintroduction a good case study to understand what shapes public support for reintroductions in a low knowledge environment. While value orientations are likely to shape reintroduction support, the lack of politicization may mean that the public does not have clear and well-identified preferences on the issue that correspond to political ideology. Opinions on the issue are also likely to be a function of demographics; elderly, rural, and lower income Americans have been found to be less supportive of bear conservation measures (Kellert, 1994). Women are likely to be more supportive of reintroduction than men, given the tendency of males to have stronger utilitarian and dominionistic attitudes toward wildlife (Kellert & Berry, 1987).

The low knowledge environment also has implications for how people assess the societal costs and benefits. If people have high information about a policy and well-formed expectations about its costs and benefits, we expect that responses about perceived costs and benefits of reintroduction will group together to reveal more nuanced patterns related to constructs such as federal control or ecological benefits. However, people in a low knowledge environment may instead respond with post-hoc rationalizations of their stated preferences on reintroductions. If so, statements about costs may group together on a single factor while statements about benefits may group on a separate factor. Assessments of costs and benefits collected after people state their support for reintroduction are likely to correlate with support for grizzly reintroduction, whether based on well-formed expectations or post-hoc rationalizations.

Finally, perceived personal threats and risk perceptions may influence attitudes (Gore, Knuth, Curtis, & Shanahan, 2007; Lubell & Vedlitz, 2006). Perceptions of individual species, their cultural and aesthetic significance, and the risks they pose have been shown to influence attitudes toward conservation practices (Kellert, Black, Rush, & Bath, 1996). Evaluations of

personal threats, such as consequences for recreation or livelihoods, likely affect the strength of support for reintroduction. Based on prior public responses to wolf (*Canis lupus*) reintroduction and recolonization efforts (Karlsson & Sjöström, 2007; Williams et al., 2002), rural Californians and those living closer to proposed reintroduction sites are likely to be less supportive of reintroduction than their urban, suburban, and more distant counterparts.

Methods

Survey Design, Representativeness, and Weighting

Using the Qualtrics online platform, we surveyed 980 Californians between February 22 and March 16, 2017 with sampling stratified by party identification and household income measures to help ensure a representative sample. The respondents were members of a panel who had volunteered to complete online questionnaires in exchange for compensation.[2] Because grizzly bear reintroduction would have the most immediate impact on rural residents, we oversampled rural residents to ensure that our statistical models could produce robust estimates of their preferences.

Table S1 provides descriptive statistics for demographics of respondents and California benchmarks from the 2016 US Census American Community Survey. The sample slightly overrepresented women, highly-educated Californians, and whites, so all results include sample weights for gender, rural/urban, education, and ethnicity, estimated using the "survey" (Lumley, 2018), "weights" (Pasek, Tahk, Culter, & Schwemmle, 2016), and "anesrake" (Pasek, 2016) packages in R, version 3.5.0 (R Development Core Team, 2018). Regression models were

[2] Sampling methodology and other supplemental information is available at https://docs.wixstatic.com/ugd/88ceb7_ffd0e67a0c2d46bb84ab70c0e73ec986.pdf .

estimated using "svyglm" function in the "survey" package (Lumley 2018) to generate standard errors that account for the loss of precision when using weighted data.

The survey instrument measured support for grizzly bear reintroduction, species awareness, value orientations, political ideology, demographic characteristics, and perceptions of the costs, benefits, and personal threats of reintroduction. It included a survey experiment using National Parks as a proxy for distance to reintroduction as, for most Californians, National Parks are in distant locations.[3] Approximately half the sample received a message indicating that proposed grizzly bear reintroduction would occur in California National Parks, while the other half of the sample received the same message, but without specifying a location. The treatment and control groups were balanced on observable covariates. We estimated the Average Treatment Effect (ATE) of the National Parks experiment with a difference-in-means estimator because the treatment was randomly assigned (Imbens & Rubin, 2015).

Measuring Support for Grizzly Bear Reintroduction

To evaluate predictors of attitudes, the dependent variable is a 7-point scale reflecting whether the respondent supports efforts to reintroduce grizzly bears into California, with responses from *strongly oppose* to *strongly support*. Respondents are first told "As you may know, grizzly bears once lived throughout much of the state, but the last grizzly in California was killed in 1922. There have been some proposals to reintroduce grizzly bears to [a number of national parks in] California." The portion in brackets is included for the national parks treatment condition.

[3] 69% of Californians live in the 19 coastal counties, while most of the National Parks are in the interior eastern portion of the state (United States Census Bureau, 2010).

Species Awareness

We measured awareness of grizzly bears, black bears (*Ursus americanus*), bald eagles (*Haliaeetus leucocephalus*), bison (*Bison bison*), and wolves in the wild in California. Respondents who correctly identified species presence or absence received a score of one for each species, and respondents who were incorrect or did not know received a zero.[4] These responses are used to approximate wildlife awareness in two ways. First, we collapsed these species-specific measures into a single additive index measuring general awareness of species existence, where more correct answers indicated higher wildlife awareness. Second, we paired species-specific awareness of grizzly bear absence in California with an index of awareness about the other species. Species awareness was measured before the treatment was assigned and before support – though asking whether respondents supported grizzly reintroduction required stating that grizzly bears are not currently in California.

Because grizzly bear awareness may be important for understanding public support for reintroduction, a logistic regression estimates the relationship between the indicator for specific grizzly bear awareness and demographic variables, political ideology, and generic species awareness to examine correlates of grizzly bear awareness. The logit estimator accounts for the dichotomous dependent variable by estimating the probability that the dependent variable is observed. Logit guarantees that estimated probabilities are between zero and one, which may not be true near the tails of the distribution when using the linear model.

[4] Black bears are present throughout California, can be brown in color like grizzly bears, and are morphologically different. Bald eagles are currently present in California. Bison are not present in the wild in California, but there is a small, managed herd on Santa Catalina Island. Wolves have migrated in and out of the state; during the time of this survey, wolves were present.

Value Orientations, Political Ideology, and Demographic Measures

We measured altruism, egoism, and biospherism with the Portrait Values Questionnaire (PVQ; Schwartz, 2003) using the mean score across four self-evaluations of how much a hypothetical person described in the survey is like the respondent on a 5-point scale ranging from *Not like me* to *Very much like me*. For example, one of the four descriptions measuring altruism asked respondents how much they are like a person described as "It's very important to him [her] to help the people around him. He[she] wants to care for other people." with pronouns matched to the gender of the respondent. This method has been proven stable across different countries, ages of respondents, and types of people (de Groot & Steg, 2007).

Political ideology was measured by asking respondents to place themselves on a 7-point scale ranging from *extremely liberal* to *extremely conservative*. A suite of standard demographic variables included the respondent's age, sex, education level, income, race/ethnicity, and urban versus rural residence. Respondents placed themselves into ordinally ranked education and income categories. Education was recoded as an indicator variable with bachelor's degree and above coded as one. Race was coded as one for white respondents and zero otherwise. Rural residence was measured by asking respondents to state whether they lived in an urban (coded 1), suburban (2), or rural (3) area (see online Table S2 for mean comparisons).

Societal and Ecological Cost and Benefit Measures and Personal Threats

Agreement with 13 statements (eight framed positively and five negatively) assessed evaluations of the societal and ecological costs and benefits of the policy, including how individuals thought grizzly reintroduction might affect the health of ecosystems, the survival of grizzly bears, property rights, local control, tourism, outdoor recreation, rural and urban residents, and a variety of livelihoods. For example, respondents were asked whether they agreed with the statement that "Grizzly bear reintroduction would harm agricultural producers" on a 5-

point scale from *strongly disagree* to *strongly agree*. These responses were analyzed using Principal Components Analysis (PCA) with varimax rotation using singular value decomposition (SVD) to identify how responses grouped together. Parallel analysis (Horn, 1965) determined the number of components to retain, and the scores resulting from the components were used in the regression models. The personal threat measures asked whether respondents anticipated needing to change their recreational behavior, and whether respondents agreed or disagreed that grizzly bear reintroduction would threaten their safety and their livelihood on the same 5-point scale.

Regression Analysis and ANOVA

For ease of interpretation, three ordinary least squares (OLS) regression models examined correlates of support for reintroduction. The dependent variable is support for grizzly bear reintroduction in California. Model 1 included the composite awareness measure, value orientations, political ideology, demographic variables, and a dummy variable indicating National Park treatment status as independent variables. Model 2 included the grizzly-specific awareness measure in place of the composite awareness measure. Model 3 included both the grizzly-specific awareness measures and the awareness composite excluding grizzly bears. Model 3 also included the components identified in the PCA and responses to the three questions about personal threats. ANOVA was used as a test of significance for factor variables with more than one level (Table S3).

Results

Grizzly Bear Presence

The most common response for questions about each species in California *except* grizzly bears was to correctly identify the current presence or absence (Figure 1). Twenty-six percent of respondents correctly reported that grizzly bears were absent from California, but nearly half

incorrectly believed that grizzly bears were present in the wild in California and the rest were unsure (see Table 1). Between 38 and 75% of respondents correctly identified the presence or absence of the other species in California. Taken together, these confirm that grizzly bear reintroduction proposals exist in a low knowledge environment.

As Table 2 with logit estimates for predictors of grizzly bear awareness shows, respondents with higher general awareness scores were more likely to correctly know that grizzly bears are absent (*odds ratio* = 1.22; $p = .03$). Additionally, older respondents were more likely to correctly indicate that grizzly bears were not in the state (*odds ratio* = 1.02; $p = .004$). Living in a suburban area relative to an urban area or a rural area increased the odds of correctly predicting grizzly bear presence by 1.65 ($p < .001$; see online Table S4 for comparison of rural, suburban, and urban). When only eagles and black bears are in the measure of awareness (online Table S5), the coefficient was no longer significant (*odds ratio* = 0.87*;* $p = .26$).

Support for Reintroduction

Sixty-three percent of respondents were at least somewhat supportive of reintroduction, with median and mean support levels of approximately five (*somewhat support*) on a 7-point scale (Table 1), and about a quarter were neither opposed nor supportive of reintroduction (Figure 2).

Other Descriptive Statistics

Respondents had median scores of 4.33, 4.00, and 3.33 on scales of one to five on the altruism, biospherism, and egoism measures, respectively. The median respondent indicated that they were somewhat likely to continue recreating in areas they commonly visit if grizzly bears were reintroduced, that they neither agreed nor disagreed that grizzly bear reintroduction would pose a threat to their personal safety, and that they somewhat disagreed with the statement that reintroduction would pose a threat to their livelihood.

National Parks (Distance) Experiment

There was no difference in support between those who received the National Parks treatment and those who did not (*ATE* = -0.03; p = .77; online Table S6). There was no evidence for the presence of heterogeneous treatment effects by political party, rural residence, or grizzly awareness (online Table S7; Table S8; Table S9). When the 7-point grizzly reintroduction support measure was collapsed to three categories indicating support, neutral, or opposition, the ATE remained small and insignificant (*ATE* = -0.01; p = .86; online Figure S1; Table S10).

Principal Components Analysis

Parallel analysis (Horn, 1965) of principal components indicated that patterns in the cost and benefit statements could be captured by two principal components, with one component reflecting positive statements and the other reflecting negative statements (Table 3). Personal threats did not load with the societal costs and benefits.

Generalized Awareness Model 1

Table 4 includes results from three regressions. Model 1 showed that general species awareness was not significantly associated with support for reintroduction. Value orientations and demographics, however, did significantly predict support. The coefficients for altruism and biospherism were positive and significantly associated with support (p = .02 and p = .003, respectively). A one-unit increase was associated with an increase in support of 0.38 and 0.36 points respectively on the 7-point scale for reintroduction support. Older respondents were less supportive of reintroduction (p < .001), and white respondents were more supportive of reintroduction than non-whites (p = .03). Substantively, an additional 50 years of age was associated with a decrease in support for reintroduction of one point and being white is

associated with an increase in support for reintroduction of 0.30 points. Surprisingly, there was no difference in support between rural and non-rural residents. Liberals were not more supportive of reintroduction than conservatives.

Grizzly-Specific Awareness Model 2

Model 2 exchanged the general awareness measure for a grizzly-specific awareness measure but kept all other variables the same. Grizzly-specific awareness was a significant predictor of support in Model 2. Individuals who thought that grizzly bears were not present were 0.80 ($p = .02$) points less supportive of reintroduction relative to those who believed that grizzly bears were present in California. Respondents who did not know their current status prior to the survey were 0.37 ($p < .001$) points less supportive of reintroduction than those who believed they existed. All other variables remain of the same sign and significance as in Model 1.

Full Model 3

The third model expanded on the first two by including personal threats and societal cost-benefit estimates from the PCA. It also included both grizzly-specific awareness and the composite awareness measure without grizzly bears.[5] Those who perceived higher societal benefits from grizzly reintroduction were more supportive ($B = 0.85$; $p < .001$). Conversely, individuals who perceived greater costs to reintroduction were significantly less supportive of it ($B = -0.3$; $p < .001$). A one-point increase in agreement that the respondent would have to change their recreational activities or in agreeing that grizzly bear reintroduction would be a threat to their livelihoods decreased support by -0.27 ($p < .001$) and -0.12 ($p = .01$), respectively. Remaining results were similar to Models 1 and 2, except that demographic characteristics were

[5] A robustness check with an ordered logit (see online Table S11) yielded roughly the same estimates, except that respondents who did not know if grizzlies existed in California were not significantly different from those who thought they do exist.

no longer significant predictors of support.[6] Additionally, the p-values for altruism and biospherism fell to $p = .09$ and $p = .1$ respectively.[7,8] Grizzly-specific awareness remained of the same sign and significance as Model 2, and general species awareness remained insignificant. An additional model with an index of personal cost statements in place of threat to safety, threat to livelihood, and continued recreation shows that the index significantly predicted support ($B = -0.11$; $p < .001$; online Table S14). All other results remained the same.

Discussion

Broadly speaking, the majority of a sample of Californians supported grizzly reintroduction, but only about one-quarter of respondents knew that grizzly bears are not present in the wild in California. This places the question of grizzly bear reintroduction in a low knowledge environment. In this low knowledge environment, those who inaccurately thought grizzlies were still present in the state, representing nearly half of the respondents, were more supportive of reintroduction than respondents who thought grizzlies were absent. This could be because people who realized that grizzlies were absent were more aware of potential problems associated with reintroduction. For example, rural respondents were more aware of grizzly bear absence than urban respondents and might well have a better understanding of the consequences of reintroduction. Alternatively, it could be because people responded to the awareness question on the basis of what they want to be true. Regardless of which mechanism is

[6] Removing value orientations and ideology and treating rural as an indicator variable investigated whether collinearity masked the effect of rural residence. There remained no significant relationship between rural residence and support for reintroduction (online Table S12).
[7] When value orientations were replaced with a measure of environmentalism from the New Environmental Paradigm (NEP; Dunlap, 2000), environmentalism was negatively related to support ($B = -0.10$; $p = .07$). The NEP scale ranges from 1 to 5, and a one unit increase in environmentalism was associated with a -0.10 decrease in support, which is very small (online Table S13).
[8] When each PCA estimate and personal threat measure was added sequentially into the model, the benefits component and recreation measure reduced the significance of value orientations to $p < .05$. The other measures did not substantially change the significance of the value orientation measures.

at play, the relationship between awareness and lack of support for reintroduction means that managers must be careful not to assume that the provision of information alone will result in public support for reintroduction proposals. Indeed, there are many public policy examples where education alone has not resulted in increased policy support (e.g., Lieu, Glauber, Fuentes-Afflick, & Lo, 1994 on vaccines). People do not assimilate information in unbiased ways (Corner, Whitmarsh, & Xenias, 2012); instead, information can be polarizing – entrenching people in their prior positions (Lord, Ross, & Lepper, 1979).

In the low knowledge environment surrounding grizzly bear reintroduction, respondents' attitudes toward reintroduction were associated with their value orientations, particularly the degree to which they were altruistic or biospheric, but not their political ideology. This suggests that respondents do not conceptualize grizzly bear reintroduction as a political issue, perhaps because the issue itself has not become politicized. On the one hand, this means that managers may be able to avoid the polarization that can occur when attitudes are shaped by ideology. On the other hand, the value orientations that they rely on are slow to change, which may in turn make these attitudes difficult to change.

When personal threats are included in the model, the relationships between value orientations and attitudes weaken, suggesting that the day-to-day consequences of reintroduction play a larger role in attitude formation. When individuals feel that their recreational activities or personal livelihood will be affected by reintroduction they are less supportive of it, and more abstract cognitive factors, such as value orientations, become less important. These same day-to-day consequences are easier to change than attitudes, especially as attitudes toward wildlife become more positive (George, Slagle, Wilson, Moeller, & Bruskotter, 2016; Manfredo, Teel, & Henry, 2009). Managers considering reintroductions may find it useful to consider presenting

ways to mitigate the possible livelihood and recreational effects before attitudes toward reintroduction become entrenched or politicized.

After respondents reported their support for reintroduction, their responses to questions about societal costs and benefits may be rationalizations of their reported stances. Questions framed as benefits loaded separately from questions framed as costs, with the former being associated with increased support and the latter being associated with decreased support. This grouping of cost statements and benefit statements suggests that respondents were rationalizing their previously stated support or opposition to grizzly bear reintroduction rather than reflecting more nuanced concepts such as trust in wildlife management agencies, general attitudes toward bears, and risk perception (Booth & Ryan, 2016; Heneghan & Morse, 2018). Many reintroductions are framed solely in terms of the costs to stakeholders and individuals (Braczkowski et al., 2018), but this suggests that it is at least as important to communicate the benefits from a reintroduction program (Zajac, Bruskotter, Wilson, & Prange, 2012).

Conclusion and Implications

Social buy-in is very important to successful reintroduction, so understanding how to manage not just the habitat, but the public, is critical. With the increasing recognition that habitat availability is only one a piece of the reintroduction landscape (Dunham, White, Allen, Marcot, & Shively, 2016), there are at least four lessons to be drawn for managers and for researchers.

First, the demonstrated lack of awareness about the absence of grizzly bears in California suggests broader challenges with reintroductions. Grizzly bears are charismatic megafauna and we would expect relatively high awareness of their absence. Yet we observe low awareness. Managers considering reintroductions of lesser-known species should expect even lower

awareness. Understanding what shapes attitudes in this low knowledge environment is critical to predicting support and to communicating effectively with the public.

Second, the received wisdom regarding reintroductions – that locals are likely to oppose them (Siegler, 2018) – does not necessarily hold, at least in the period before a reintroduction has become politicized. Controlling for their greater awareness of grizzly bears, rural residents were not less supportive of grizzly bear reintroduction. In addition, respondents who were told that grizzly bears would be reintroduced in National Parks (likely far from them) were not more supportive. This is in contrast to the finding in wolf reintroduction in the US (Bath, 1989) and wolf recolonization in Europe (Karlsson & Sjöström, 2007) that larger distances from recolonization result in higher support. This suggests that managers need to refine our understanding of the political geography of reintroductions.

Third, managers and researchers can expect that value orientations, which shape attitudes toward many issues, pertain to proposed reintroductions. Value orientations are slow to change, so public outreach on reintroduction issues should instead emphasize mitigation of the threats of proposed reintroduction and possible benefits, particularly to people who perceive threats to their livelihoods or recreational activities. Framing reintroduction in terms of the ecological benefits gained may be important for those with biospheric value orientations. For those with altruistic and egoistic value orientations, emphasizing social or personal benefits may be more important for facilitating support.

Fourth, that respondents rationalized the ecological and social costs and benefits of reintroduction suggests that managers and researchers should develop information about reintroduction costs and benefits as early as possible (Clark, Huber, & Servheen, 2002), perhaps even prior to introducing management proposals. Even in low knowledge environments, the public appears willing to express opinions that may be difficult to change, especially after they

have rationalized those attitudes with consideration of the societal and ecological costs and benefits. A focus on communicating benefits, as opposed to mitigating risk, can be an important tool in increasing tolerance for predators (Bruskotter & Wilson, 2014; Slagle, Zajac, Bruskotter, Wilson, & Prange, 2013). Moreover, media messaging about human-wildlife conflict can influence awareness and perceived risks (Bhatia, Athreya, Grenyer, & Macdonald, 2013). Managers are in a position to provide early information that would allow the public to rely on a well-informed assessment of the potential impacts of reintroduction.

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References

Aipanjiguly, S., Jacobson, S. K., & Flamm, R. (2003). Conserving Manatees: Knowledge, Attitudes, and Intentions of Boaters in Tampa Bay, Florida. *Conservation Biology*, *17*, 1098–1105.

Allport, G. W. (1961). Values and our youth. *Teachers College Record*, *63*, 211–219.

Bardi, A., & Schwartz, S. H. (2003). Values and Behavior: Strength and Structure of Relations. *Personality and Social Psychology Bulletin*, *29*, 1207–1220.

Bath, A. J. (1989). The public and wolf reintroduction in Yellowstone National Park. *Society and Natural Resources*, *2*, 297–306.

Bhatia, S., Athreya, V., Grenyer, R., & Macdonald, D. W. (2013). Understanding the Role of Representations of Human-Leopard Conflict in Mumbai through Media-Content Analysis. *Conservation Biology*, *27*, 588–594.

Booth, A. L., & Ryan, D. (2016). Goldilocks Revisited: Public Perceptions of Urban Bears in Northern British Columbia. *Human Dimensions of Wildlife*, *21*, 460–470.

Braczkowski, A. R., O'Bryan, C. J., Stringer, M. J., Watson, J. E. M., Possingham, H. P., & Beyer, H. L. (2018). Leopards provide public health benefits in Mumbai, India. *Frontiers in Ecology and the Environment*, *16*, 176–182.

Bruskotter, J. T., & Wilson, R. S. (2014). Determining where the wild things will be: Using psychological theory to find tolerance for large carnivores. *Conservation Letters*, *7*, 158–165.

Casey, A. L., Krausman, P. R., Shaw, W. W., & Shaw, H. G. (2005). Knowledge of and attitudes toward mountain lions: A public survey of residents adjacent to Saguaro National Park, arizona. *Human Dimensions of Wildlife*, *10*, 29–38.

Center for Biological Diversity. (2014). *Petition for a Recovery Plan for the Grizzly Bear (Ursus arctos horribilis) Across Its Native Range in the Conterminous United States*.

Clark, J. D., Huber, D., & Servheen, C. (2002). Bear Reintroductions : Lessons and Challenges. *Ursus*, *13*, 335–345.

Corner, A., Whitmarsh, L., & Xenias, D. (2012). Uncertainty, scepticism and attitudes towards climate change: Biased assimilation and attitude polarisation. *Climatic Change*, *114*, 463–478.

Daniels, D. P., Krosnick, J. a., Tichy, M. P., & Tompson, T. (2012). Public Opinion on Environmental Policy in the United States. In M. Kraft & S. Kamieniecki (Eds.), *Handbook of US Environmental Policy* (pp. 461–486). New York, NY, NY: Oxford University Press.

de Groot, J. I. M., & Steg, L. (2007). Value Orientations and Environmental Beliefs in Five Countries: Validity of an Instrument to Measure Egoistic , Altruistic and Biospheric Value Orientations. *Journal of Cross-Cultural Psychology*, *38*, 318–332.

Dietz, T., Dan, A., & Shwom, R. (2007). Support for climate change policy: social psychological and social structural influences. *Rural Sociology*, *72*, 185–214.

Dunham, J. B., White, R., Allen, C. S., Marcot, B. G., & Shively, D. (2016). The reintroduction landscape: Finding success at the intersection of ecological, social, and institutional dimensions. In D. S. Jachowski, J. Millspaugh, P. L. Angermeier, & R. Slotow (Eds.), *Reintroduction of fish and wildlife populations*. Oakland, CA: University of California Press.

Fishbein, M., & Ajzen, I. (1975). *Belief, Attitude, Intention, and Behavior: An Introduction to Theory and Research*. Reading, Massachusetts: Addison Wesley Publishing Company.

Fletcher, S., Potts, J. S., Heeps, C., & Pike, K. (2009). Public awareness of marine environmental issues in the UK. *Marine Policy*, *33*, 370–375.

Fulton, D. C., Manfredo, M. J., & Lipscomb, J. (1996). Wildlife value orientations: A conceptual and measurement approach. *Human Dimensions of Wildlife*, *1*, 24–47.

Gagnon Thompson, S. C., & Barton, M. A. (1994). Ecocentric and anthropocentric attitudes toward the environment. *Journal of Environmental Psychology*, *14*, 149–157.

George, K. A., Slagle, K. M., Wilson, R. S., Moeller, S. J., & Bruskotter, J. T. (2016). Changes in attitudes toward animals in the United States from 1978 to 2014. *Biological Conservation*, *201*, 237–242.

Gilens, M., & Murakawa, N. (2002). *Elite Cues and Political Decision-Making. Political Decision-Making, Deliberation and Participation* (Vol. 6).

Gore, M. L., Knuth, B. A., Curtis, P. D., & Shanahan, J. E. (2007). Factors influencing risk perception associated with human-black bear conflict. *Human Dimensions of Wildlife, 12, 133-136*.

Heneghan, M. D., & Morse, W. (2018). Finding our bearings: Understanding public attitudes toward growing black bear populations in Alabama. *Human Dimensions of Wildlife*, *23*, 54–70.

Holian, M. J., & Kahn, M. E. (2015). Household Demand for Low Carbon Public Policies : *Journal of the Association of Environmental and Resource Economists*, *2*(2).

Horn, J. L. (1965). A rationale and test for the number of factors in factor analysis. *Psychometrika*, *30*, 179–185.

Imbens, G. W., & Rubin, D. B. (2015). *Causal Inference in Statistics, Social, and Biomedical Sciences*. Cambridge, UK: Cambridge University Press.

Karlsson, J., & Sjöström, M. (2007). Human attitudes towards wolves, a matter of distance. *Biological Conservation*, *137*, 610–616.

Kellert, S. R. (1984). American-Attitudes Toward and Knowledge of Animals: An Update. In M. W. Fox & L. D. Mickley (Eds.), *Advances in Animal Welfare Science* (pp. 177–213). Washington, DC: The Humane Society of the United States.

Kellert, S. R. (1994). Public Attitudes toward Bears and Their Conservation. In *Bears: Their Biology and Management* (Vol. 9, pp. 43–50). International Association for Bear Research and Management.

Kellert, S. R., & Berry, J. K. (1987). Attitudes , Knowledge , and Behaviors toward Wildlife as Affected by Gender. *Wildlife Society Bulletin*, *15*, 363–371.

Kellert, S. R., Black, M., Rush, C. R., & Bath, A. J. (1996). Human Culture and Large Carnivore Conservation in North America. *Conservation Biology*, *10*, 977–990.

Kusmanoff, A. M., Hardy, M. J., Fidler, F., Maffey, G., Raymond, C., Reed, M. S., … Bekessy, S. A. (2016). Framing the private land conservation conversation: Strategic framing of the benefits of conservation participation could increase landholder engagement. *Environmental Science and Policy*, *61*, 124–128.

Lieu, T. A., Glauber, J. H., Fuentes-Afflick, E., & Lo, B. (1994). Effects of Vaccine Information Pamphlets on Parents' Attitudes. *Archives of Pediatrics & Adolescent Medicine*, *148*, 921.

Loomis, J. B., Bair, L. S., & Gonzalez-Caban, A. (2001). Prescribed Fire and Public Support: Knowledge Gained, Attitudes Changed in Florida. *Journal of Forestry*, *99*, 18–22.

Lord, C. G., Ross, L., & Lepper, M. R. (1979). Biased assimilation and attitude polarization: The effects of prior theories on subsequently considered evidence. *Journal of Personality and Social Psychology*, *37*, 2098–2109.

Lubell, M., & Vedlitz, A. (2006). Collective Action, Environmental Activism, and Air Quality Policy. *Political Research Quarterly*, *59*, 149–160.

Lumley, T. (2018). Survey. Retrieved from http://r-survey.r-forge.r-project.org/survey

Manfredo, M. J., Teel, T. L., & Henry, K. L. (2009). Linking society and environment: A multilevel model of shifting wildlife value orientation in the western United States. *Social Science Quartely*, *90*, 407–427.

Pasek, J. (2016). anesrake: ANES Raking Implementation. Retrieved from https://cran.r-project.org/package=anesrake

Pasek, J., Tahk, A., Culter, G., & Schwemmle, M. (2016). weights: Weighting and Weighted Statistics. Retrieved from https://cran.r-project.org/package=weights%0A%0A

R Development Core Team. (2018). R: A Language and Environment for Statistical Computing. (R. D. C. Team, Ed.), *R Foundation for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reading, R. P., Clark, T. W., & Kellert, S. R. (1991). Towards an Endangered Species Reintroduction Paradigm. *Endangered Species Update*, *8*, 1–4.

Roccas, S., Sagiv, L., Schwartz, S. H., & Knafo, A. (2002). The Big Five Personality Factors and Personal Values. *Personality and Social Psychology Bulletin*, *28*, 789–801.

Rokeach, M. (1973). *The nature of human values*. New York, NY: Free Press.

Scheufele, D. A., & Lewenstein, B. V. (2005). The public and nanotechnology: How citizens make sense of emerging technologies. *Journal of Nanoparticle Research*, *7*, 659–667.

Schwartz, S. H. (2003). A Proposal for Measuring Value Orientations across Nations. In *Questionnaire Package of the European Social Survey* (pp. 259–319).

Schwartz, S. H. (2010). Basic values: How they motivate and inhibit prosocial behavior. In M. Mikulincer & P. R. Shaver (Eds.), *Prosocial motives, emotions, and behavior: The better angels of our nature* (pp. 221–241). Washington, DC: US: American Psychological Association.

Schwartz, S. H., & Bardi, A. (1997). Influences of Adaptation to Communist Rule on Value Priorities in Eastern Europe. *Political Psychology*, *18*, 385–410.

Schwartz, S. H., Caprara, G. V., & Vecchione, M. (2010). Basic Personal Values, Core Political Values, and Voting: A Longitudinal Analysis. *Political Psychology*, *31*, 421–452.

Schwartz, S. H., Lehmann, A., & Roccas, S. (1999). Multimethod probes of basic human values. *Social Psychology and Culture Context: Essays in Honor of Harry C. Triandis*, 107–123.

Selge, S., Fischer, A., & van der Wal, R. (2011). Public and professional views on invasive non-native species – A qualitative social scientific investigation. *Biological Conservation*, *144*, 3089–3097.

Siegler, K. (2018). *Ranchers Sour on Trump Administration Over Proposal to Bring Back Grizzly Bears*. National Public Radio. Retrieved from https://www.npr.org/2018/05/11/609541010/ranchers-sour-on-trump-administration-over-proposal-to-bring-back-grizzly-bears

Slagle, K., Zajac, R., Bruskotter, J. T., Wilson, R. S., & Prange, S. (2013). Building tolerance for bears: A communications experiment. *Journal of Wildlife Management*, *77*, 863–869.

Sniderman, P. M., Brody, R. A., & Tetlock, P. E. (1991). *Reasoning and Choice: Explorations in Political Psychology*. New York, NY: Cambridge University Press.

Stern, P. C., & Dietz, T. (1994). The Value Basis of Environmental Concern. *Journal of Social Issues*, *50*, 65–84.

Stoutenborough, J. W., Sturgess, S. G., & Vedlitz, A. (2013). Knowledge, risk, and policy support: Public perceptions of nuclear power. *Energy Policy*, *62*, 176–184.

Trevethan, R. (2017). Deconstructing and Assessing Knowledge and Awareness in Public Health Research. *Frontiers in Public Health*, *5*, 16–19.

United States Census Bureau. (2010). 2010 Census. US Census Bureau. Retrieved from http://www.census.gov/2010census/data/

Vaske, J. J., & Donnelly, M. P. (1999). A value-attitude-behavior model predicting wildland preservation voting intentions. *Society and Natural Resources*, *12*, 523–537.

Vaske, J. J., Donnelly, M. P., Williams, D. R., & Jonker, S. (2001). Demographic influences on environmental value orientations and normative beliefs about national forest management. *Society and Natural Resources*, *14*, 761–776.

Whittaker, D., Vaske, J. J., & Manfredo, M. J. (2006). Specificity and the cognitive hierarchy: Value orientations and the acceptability of urban wildlife management actions. *Society and Natural Resources*, *19*, 515–530.

Williams, C. K., Ericsson, G., & Heberlein, T. A. (2002). A quantitative summary of attitudes toward wolves and their reintroduction (1972-2000). *Wildlife Society Bulletin*, *30*, 575–584.

Wilson, C., & Tisdell, C. (2005). What Role Does Knowledge of Wildlife Play in Providing Support for Species' Conservation? *Journal of Social Sciences*, *1*, 47–51.

Zajac, R. M., Bruskotter, J. T., Wilson, R. S., & Prange, S. (2012). Learning to live with black bears: A psychological model of acceptance. *Journal of Wildlife Management*, *76*, 1331–1340.

Zelezny, L. C. (1999). Educational interventions that improve environmental behaviors: A meta-analysis. *Journal of Environmental Education*, *31*, 5–14.

Figures

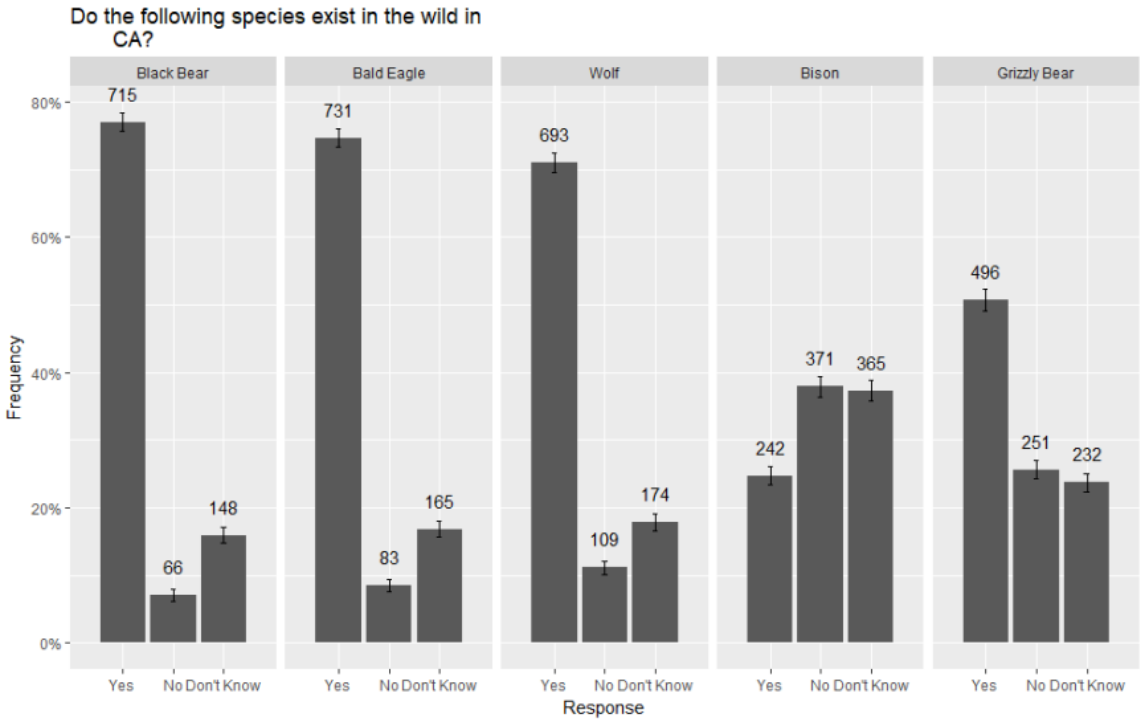


Figure 1*:* Respondent awareness of wildlife presence in California. Black bears, bald eagles, and wolves are present in the wild in California; bison and grizzly bears are not. Vertical bars represent standard errors. Numbers above the bars represent total number of responses for each category. Total responses for each species were 929 for black bears, 979 for bald eagles, 976 for wolves, 978 for bison, and 979 for grizzly bears.

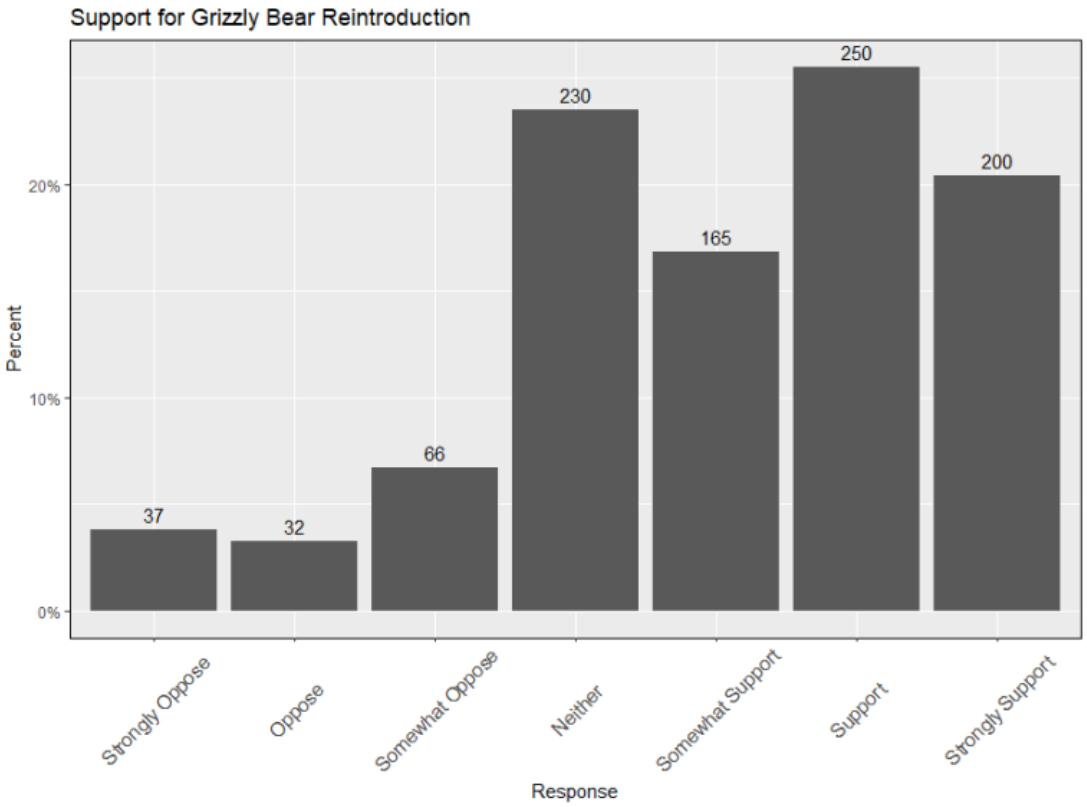


Figure 2: Respondent support for grizzly bear reintroduction in California on a 1-7 scale. Mean support level is somewhat supportive (5.05). Numbers above the bars represent the total number of responses in each category

Tables

Table 1: Summary Statistics

Variable	Median	Mean	Min	Max	St. Dev.
Support for Grizzly Reintroduction	5 (Somewhat Support)	5.05	1	7	1.57
Species Awareness	3	2.56	0	4	1.01
Grizzly Presence Indicator	0	.25	0	1	.44
Benefits Component	0.005	0	-3.27	2.39	1
Costs Component	-0.095	0	-3.27	2.86	1
Altruism	4.33	4.16	1.67	5	0.67
Biospherism	4	4	1	5	0.71
Egoism	3.33	3.16	1	5	0.88
Recreation	2 (Somewhat likely to continue)	2.5	1	5	1.34
Threat to Safety	3 (Neither agree nor disagree)	2.78	1	5	1.27
Threat to Livelihood	2 (Somewhat disagree)	2.24	1	5	1.24
Ideology	4 (Moderate)	3.68	1	7	1.70

Note. Support for reintroduction is measured on a 7-point scale. Species awareness is a composite indicator of awareness of all species except for grizzly bears. Grizzly presence is the indicator variable for whether a respondent correctly predicted grizzly bear presence. This is different from the categorical variable measuring grizzly bear awareness that is used to predict support for reintroduction (Table 4), where the variable's levels correspond to not knowing whether grizzlies are present, believing they are present, or correctly identifying that they are not present (see Figure 1). Benefits and costs components are PCA scores. Altruism, biospherism, and egoism are continuous measures of each value orientation. Recreation, threat to safety, and threat to livelihood are measured on 5-point scale, and ideology is a 7-point scale.

Table 2: Predicting Awareness of Grizzly Bear Presence

Variable	*B*	*SEB*	*Odds Ratio*
Constant	-3.40***	0.53	0.03
Age	0.02***	0.02	1.02
Female	-0.16	0.18	0.85
College Graduate	0.19	0.19	1.21
Income	0.05	0.04	1.05
Rural	0.50***	0.12	1.65
Ideology	0.03	0.05	1.03
Awareness Score	0.20**	0.09	1.22
Pseudo R^2	.06		
N	769		

Note. *p < .1; **p < .05; ***p < .01

Note. Logistic regression. Dependent variable is grizzly-specific awareness indicator variable coded as 1 if respondent answered *no* and 0 they responded either *yes* or *don't know*.

Table 3: Principal Components Analysis

	Component 1	**Component 2**	**Cronbach's α**
Benefits			.89
People have a responsibility to ensure the survival of grizzly bears	**.60**	-.08	
Grizzly bear reintroduction would help make California forests healthier.	**.81**	-.14	
Grizzly bear reintroduction would benefit the California economy by increasing tourism.	**.76**	-.01	
Grizzly bear reintroduction would benefit other species.	**.79**	-.12	
Grizzly bear reintroduction would help prevent their extinction.	**.64**	-.13	
Grizzly bear reintroduction would benefit outdoor recreation.	**.79**	-.05	
Grizzly bear reintroduction would benefit urban residents.	**.74**	.16	
Grizzly bear reintroduction would benefit rural residents.	**.80**	.04	
Costs			.76
Grizzly bear reintroduction would lead to an increased role for the federal government.	.14	**.52**	
Grizzly bear reintroduction would threaten property rights on private lands	-.20	**.81**	

Grizzly bear reintroduction would reduce local control over public lands.	.18	**.70**
Grizzly bear reintroduction would negatively impact ranchers.	-.35	**.74**
Grizzly bear reintroduction would harm agricultural producers.	-.18	**.76**
Note. Loadings from PCA with varimax rotation. Loadings greater than .5 are bolded.		

Table 4: Measuring Support for Reintroduction

Variable	*Model 1*		*Model 2*		*Model 3*		
	B	***SE B***	***B***	***SE B***	***B***	***SE B***	***β***
Constant	2.93***	0.75	3.28***	0.77	5.36***	0.64	
Species Awareness	0.05	0.055	-	-	0.00	0.04	0.00
Grizzly Existence (No)	-	-	-0.80***	0.15	-0.38***	0.11	-0.20
Grizzly Existence (Don't Know)	-	-	-0.37**	0.15	-0.18*	0.11	-0.25
Benefit Component	-	-	-	-	0.85***	0.06	0.53
Cost Component	-	-	-	-	-0.30***	0.06	-0.13
Altruism	0.38**	0.16	0.39**	0.16	0.23*	0.14	0.11
Biospherism	0.36***	0.12	0.30**	0.12	-0.14*	0.09	-0.08
Egosim	0.02	0.08	0.01	0.08	0.06	0.06	0.05
Recreation	-	-	-	-	-0.27***	0.04	-0.21
Threat to Safety	-	-	-	-	0.05	0.05	0.03
Threat to Livelihood	-	-	-	-	-0.12***	0.05	-0.13
Ideology	-0.04	0.04	-0.05	0.04	0.02	0.03	0.00
College Graduate	-0.07	0.13	-0.05	0.13	-0.08	0.09	-0.04
Rural	-0.04	0.09	0.03	0.09	0.02	0.06	0.00
Female	-0.22	0.13	-0.24*	0.13	-0.03	0.10	-0.29
Age	-0.02***	0.00	-0.02***	0.00	0.00	0.00	0.00

Income	0.03	0.04	0.04	0.03	0.02	0.02	0.00
White	0.30**	0.14	0.29**	0.13	0.08	0.10	0.03
Treatment	-0.11	0.12	-0.12	0.12	-0.03	0.09	-0.01
R^2	.16		.19		.60		
N	770		769		764		

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. Dependent variable is 7-point scale for support of Grizzly bear reintroduction in California. Standardized coefficients for Model 3 are located under column titled β.

Supplemental Material

Supplement 1: Qualtrics Panel Sampling Methodology

The participants were a non-probability sample of Californian adults aged 18 or older with sampling stratified on household income and party identification to help ensure respondents representative of the California population. Participants were drawn from commercial online panels aggregated by Qualtrics from third-parties. The panels include people living in all U.S. states, but our sample includes only Californians. Qualtrics or its partners invite the participants and pay the participant incentives for completing a questionnaire. These panels consist of convenience samples of individuals who have elected to opt-in to participate in surveys in exchange for points, which they may exchange for gift cards from retail merchants, for cash, to enter raffles, for gift cards, or for products. Participants in the Qualtrics panel receive an incentive based in part on the length of the survey. Participants are invited with an email, which does not include details about the survey. The panel partners maintain profiles of the panelists that are used for stratification. These panelists must submit an initial registration form and use a double opt-in requirement. To avoid duplication, Qualtrics checks IP addresses. For more information, please visit:
http://success.qualtrics.com/rs/qualtrics/images/ESOMAR%2028%202014.pdf

Supplement 2: Survey Questions

Demographics, Education and Employment

In which state do you currently reside?

Which of the following best describes the area where you live?

- Urban
- Suburban
- Rural

How old are you?

What is your sex?

What is the highest level of school you have completed or the highest degree you have received?

- Less than high school degree
- High school graduate (high school diploma or equivalent including GED)
- Some college but no degree
- Associate degree in college (2-year)
- Bachelor's degree in college (4-year)
- Master's degree
- Doctoral degree
- Professional degree (JD, MD)

Information about income is very important to understand. Would you please give your best guess? Please indicate the answer that includes your entire household income during the past year before taxes.

- Less than $20,000
- $20,000 to $39,999
- $40,000 to $59,999
- $60,000 to $74,999
- $75,000 to $99,999
- $100,000 to $149,999
- $150,000 or more

Please indicate your occupation:

- Management, professional, and related
- Service
- Sales and office
- Farming, fishing, and forestry
- Construction, extraction, and maintenance
- Production, transportation, and material moving
- Government
- Retired
- Unemployed

Choose one or more races that you consider yourself to be:

- ☐ White
- ☐ Black or African American
- ☐ American Indian or Alaska Native
- ☐ Asian
- ☐ Native Hawaiian or Pacific Islander
- ☐ Other _____

Are you Spanish, Hispanic, or Latino or none of these?

- o Yes
- o None of these

Political Preference and Affiliation

Generally speaking, do you consider yourself a Republican, a Democrat, an Independent, or something else?

- o Republican
- o Democrat
- o Independent
- o Other; Please Specify _____

If responded Independent: Do you think of yourself as closer to the Republican Party or to the Democratic party?

- o Closer to the Republican Party
- o Closer to the Democratic Party
- o Neither

If responded Democratic: Would you consider yourself a strong Democrat or a not very strong Democrat?

- o Strong Democrat
- o Not very strong Democrat

If responded Republican: Would you consider yourself a strong Republican or a not very strong Republican?

- o Strong Republican
- o Not very strong Republican

Where would you place yourself on this scale, or haven't you thought about it much?

- o Extremely liberal
- o Liberal
- o Somewhat liberal
- o Moderate; middle of the road
- o Somewhat conservative

- Conservative
- Extremely conservative
- Haven't thought much about this

Portrait Values Questionnaire (PVQ)

Several different types of people are described below. Please read the descriptions thoroughly and think about how each person is or is not like you. There are no right answers, simply read the description and choose the best fit to the right.

	Very much like me	Like me	Somewhat like me	Not like me	Not like me at all
It's very important to him/her to help the people around him/her. He/she wants to care for other people.	☐	☐	☐	☐	☐
He/she thinks it is important that every person in the world be treated equally. He/she wants justice for everybody, even for people he/she doesn't know.	☐	☐	☐	☐	☐
He/she strongly believes that people should care for nature. Looking after the environment is important to him/her.	☐	☐	☐	☐	☐
It is important to him/her to adapt to nature and fit into it. He/she believes that people should not change nature.	☐	☐	☐	☐	☐
It is important to him/her to respect the earth. He/she believes that humans should live in harmony with other species.	☐	☐	☐	☐	☐
This is a control question, please select "Not like me."	☐	☐	☐	☐	☐
It is important to him/her to be rich. He/she wants to have a lot of money and expensive things.	☐	☐	☐	☐	☐
It is important to him/her to be in charge and tell others what to do. He/she wants people to do what he says.	☐	☐	☐	☐	☐
He/she always wants to be the one who makes the decisions. He/she likes to be the leader.	☐	☐	☐	☐	☐
He/she wants everyone to be treated fairly, even people he/she doesn't know. It is important to	☐	☐	☐	☐	☐

him/her to protect the weak in society.	

[Pronouns were matched to the gender of the respondent.]

New Environmental Paradigm (NEP)

Please read each of the following statements and indicate whether you strongly agree, mostly agree, are unsure, mostly disagree, or strongly disagree. There are no right or wrong answers.

	strongly agree	mostly agree	Unsure	mostly disagree	strongly disagree
Humans are severely abusing the environment.	□	□	□	□	□
The balance of nature is strong enough to cope with the impacts of modern industrial nations.	□	□	□	□	□
The so-called "ecological crisis" facing humankind has been greatly exaggerated	□	□	□	□	□
If things continue on their present course, we will soon experience a major ecological catastrophe.	□	□	□	□	□
The earth is like a spaceship with limited room and resources.	□	□	□	□	□

Again, read each of the following statements and indicate whether you strongly agree, mostly agree, are unsure, mostly disagree, or strongly disagree. There are no right or wrong answers.

	strongly agree	mostly agree	Unsure	mostly disagree	strongly disagree
If people have the vision and ability to acquire property, they should be allowed to enjoy it.	□	□	□	□	□

Everyone should have an equal chance to succeed and fail without government interference.	☐	☐	☐	☐	☐
Co-operation with others rarely works. It seems that no matter who you vote for in an election, things remain pretty much the same.	☐	☐	☐	☐	☐
If people have the vision and ability to acquire property, they should be allowed to enjoy it.	☐	☐	☐	☐	☐

Species Awareness and Reintroduction Support

Do the following wildlife species exist in the wild in California?

	Yes	No	Don't Know
Grizzly bears	☐	☐	☐
Bald eagles	☐	☐	☐
Bison	☐	☐	☐
Wolves	☐	☐	☐
Black bears	☐	☐	☐

Grizzly Reintroduction Treatment 1(no national park reference): As you may know, grizzly bears once lived throughout much of the state, but the last grizzly in California was killed in 1922. There have been some proposals to reintroduce grizzly bears to California.

Grizzly Reintroduction Treatment 1(national park reference): As you may know, grizzly bears once lived throughout much of the state, but the last grizzly in California was killed in 1922. There have been some proposals to reintroduce grizzly bears to a number of national parks in California.

Do you oppose or support efforts to reintroduce grizzly bears to California?

- o Strongly support
- o Support

- Somewhat support
- Neither support nor oppose
- Somewhat oppose
- Oppose
- Strongly oppose

In the last year, which of the following outdoor recreational activities have you participated in? (check all that apply)

- ☐ Fishing
- ☐ Hunting
- ☐ Hiking
- ☐ Bird watching/wildlife viewing
- ☐ Camping in a campground
- ☐ Backpacking
- ☐ Climbing, mountaineering, or other alpinism
- ☐ Ocean activities such as surfing, kayaking, boating, diving, etc.
- ☐ Skiing or snowboarding
- ☐ Other, please specify_____

If grizzly bears were reintroduced in the outdoor areas where you currently recreate, how likely would you be to continue to use these areas?

- Very likely to continue using areas
- Somewhat likely to continue using areas
- Neither likely nor unlikely to continue using areas
- Somewhat likely to discontinue using areas
- Very likely to discontinue using areas

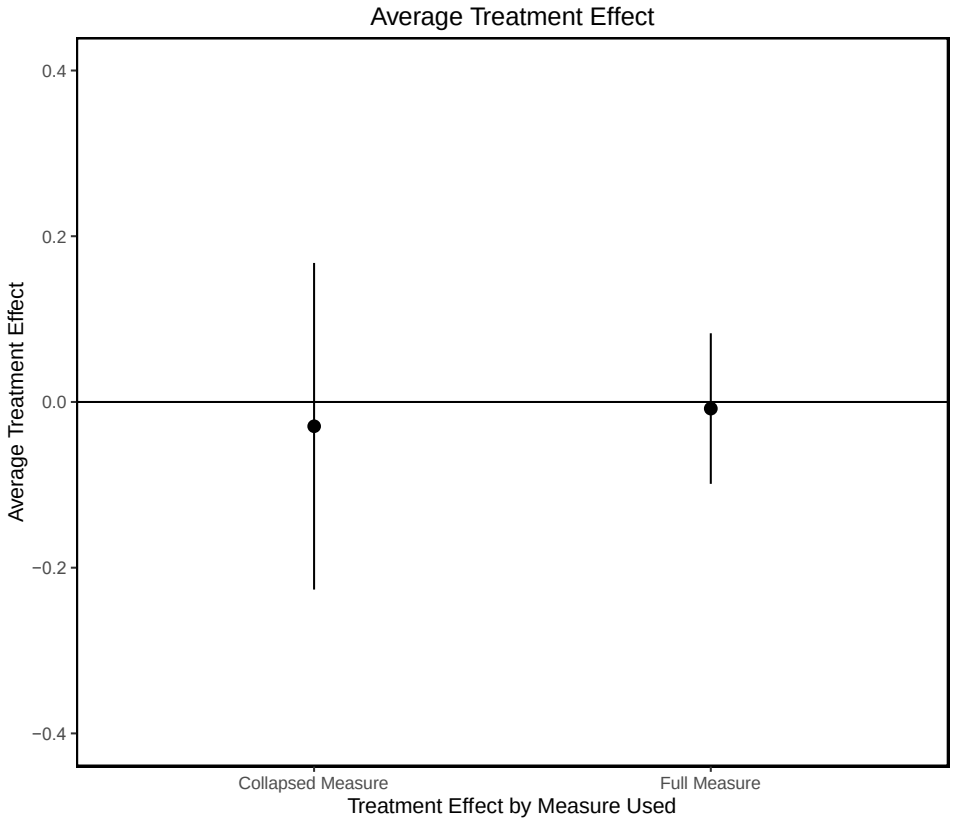
We'd like to understand more about how you think about grizzly bears. Please tell us how much you agree or disagree with each of the following statements about grizzly bear reintroduction in California.

	strongly agree	mostly agree	unsure	mostly disagree	strongly disagree
People have a responsibility to ensure the survival of grizzly bears.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would help make California forests healthier.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would pose a threat to my safety.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would pose a threat to my livelihood.	☐	☐	☐	☐	☐

Grizzly bear reintroduction would benefit the California economy by increasing tourism.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would lead to an increased role for the federal government.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would threaten property rights on private lands.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would benefit other species.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would help prevent their extinction.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would reduce local control over public lands.	☐	☐	☐	☐	☐
This is a control question, please select "Strongly agree."	☐	☐	☐	☐	☐
Grizzly bear reintroduction would negatively impact ranchers.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would benefit outdoor recreation.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would harm agricultural producers.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would benefit urban residents.	☐	☐	☐	☐	☐
Grizzly bear reintroduction would benefit rural residents.	☐	☐	☐	☐	☐

Supplemental Figures

Figure S1: Average Treatment Effect



Note. 95% confidence intervals denoted by error bars. Collapsed measure merges the 7-point scale for support for reintroduction into a 3-point scale indicating no support, neither support or support, or support. Full measure uses 7-point scale. N = 980.

Supplemental Tables

Table S1: Representativeness (Survey and California)

Variable	**Survey**	**California**
Age (Median)	40***	36
Female over 18 (Percent)	62.1%***	50.3%
College (Percent with Bachelor's degree or higher)	45%***	32%
White Only (Percent)	68%***	61.3%
Household Income (Median, in thousands)	40 – 60	63.8
Republican (Percent)	28%	26%
Democrat (Percent)	48%	45%
Independent (Percent)	21%*	25%

Note: California demographic statistics taken from 2016 US Census American Community Survey. The measure of household income is ordinal, with each level corresponding to an income bracket, rather than a specific amount, and income brackets used in the US Census do not overlap with ours. Chi-square tests check sample representativeness for Female, College, and White only, and a two-sided Wilcoxon signed rank tests for representativeness of Age. We compare the median household income bracket in our sample to the median household income of Californians as a whole, but do not test for representativeness. In each test, the null hypothesis is that there is no difference between the sample and California as a whole. Party identification information taken from the Public Policy Institute of California's January 2017 survey of Californians. We do not weight by age because age categories in the sample do not overlap correctly with US Census age estimates.
*$p < .05$; **$p < .01$; ***$p < .001$.

Table S2: Means for Urban and Rural Residents

Variable	Urban Mean	Rural Mean	*T-statistic*
Awareness Score	2.43	2.77	-4.15***
Altruism	4.23	4.14	1.69
Biospherism	4.05	4.00	0.72
Egoism	3.28	3.04	3.42***
Recreation	2.42	2.44	-0.18
Safety	2.83	2.84	0.90
Livelihood	2.44	2.11	3.22***
Ideology	3.32	4.02	-4.69***

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. For each variable a difference in means test is performed.

Table S3: Analysis of Deviance (Model 3 Type II tests)

Variable	*Degrees of Freedom*	*Chi Square*	*P-value*
General Awareness	1	0.00	.98
Grizzly Awareness	2	12.79	.002**
Benefit Component	1	181.12	<.001***
Cost Component	1	29.13	<.001***
Altruism	1	2.96	.09*
Biospherism	1	2.73	.10*
Egoism	1	1.22	.27
Recreation	1	42.77	<.001***
Threat to Safety	1	0.76	.38
Threat to Livelihood	1	6.84	.01***
Ideology	1	0.39	.53
College Graduate	1	0.72	.40
Rural	1	0.10	.76
Female	1	0.09	.77
Age	1	0.75	.39
Income	1	0.60	.44
White	1	0.76	.38
Received Treatment	1	0.12	.73

Note. *$p < .1$; **$p < .05$; ***$p < .01$

Table S4: Awareness of Grizzly Presence by Urbanicity

	Grizzly Bear Presence in California		
Urbanicity	No	Yes	Don't Know
Urban	18%	58%	25%
Suburban	24%	53%	22%
Rural	38%	37%	25%

Note. Rows are rounded and may not sum to 100%. A chi-square test rejects the null of no dependence between awareness of grizzly bear presence and urbanicity ($\chi^2 = 37.2$, $df = 4$, $p < .001$).

Table S5: Predicting Awareness of Grizzly Bear Presence (Logit)

Variable	***B***	***SE B***	***Odds Ratio***
Constant	-2.88***	0.50	0.06
Age	0.02***	0.01	1.02
Female	-0.19	0.18	0.83
College Graduate	0.23	0.19	1.26
Income	0.05	0.04	1.05
Rural	0.56***	0.12	1.74
Ideology	0.03	0.05	1.03
Awareness Score	-0.14	0.12	0.87
Pseudo R^2	.05		
N	769		

Note. *$p < .1$; **$p < .05$; ***$p < .01$
Note. Dependent variable is grizzly-specific awareness indicator variable coded as 1 if respondent answered *no* and 0 they responded either *yes* or *don't know*. Awareness Score is a composite measure with eagles and black bears only; it does not include wolves and bison.

Table S6: Average Treatment Effect for National Parks Experiment

Variable	*B*	*SE B*
Treatment	-0.03	0.10

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. The intercept is 5.05***, $N = 980$, and $R^2 < .00$. Dependent variable is 7-point scale for support of grizzly bear reintroduction in California.

Table S7: Heterogeneous Treatment Effects by Party

	Democrats		Republicans		Independents	
Variable	***B***	***SE B***	***B***	***SE B***	***B***	***SE B***
Treatment	-0.11	0.17	-0.13	0.23	0.18	0.24

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. Party identification is interacted with treatment status and treatment effects are reported. The intercept is 5.08***, $N = 980$, and $R^2 < .00$. Dependent variable is 7-point scale for support of grizzly bear reintroduction in California.

Table S8: Heterogeneous Treatment Effects by Urbanicity

	Urban		Suburban		Rural	
Variable	***B***	***SE B***	***B***	***SE B***	***B***	***SE B***
Treatment	-0.08	0.18	-0.08	0.18	0.02	0.25

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. Urbanicity is interacted with treatment status and treatment effects are reported. The intercept is 5.32***, $N = 980$, and $R^2 < .00$. Dependent variable is 7-point scale for support of grizzly bear reintroduction in California.

Table S9: Heterogeneous Treatment Effects by Grizzly Awareness

	Yes		No		Don't Know	
Variable	***B***	***SE B***	***B***	***SE B***	***B***	***SE B***
Treatment	-0.08	0.15	0.14	0.29	-0.23	0.30

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. Grizzly awareness is interacted with treatment status and treatment effects are reported. The intercept is 5.49***, $N = 980$, and $R^2 < .00$. Dependent variable is 7-point scale for support of grizzly bear reintroduction in California.

Table S10: Average Treatment Effect for Survey Experiment with Collapsed Dependent Variable Scale (OLS)

Variable	*B*	*SE B*
Treatment	-0.01	0.05
Note. *p < .1; **p < .05; ***p < .01.		
Note. The intercept is 2.49***, N = 980, and R^2 < .00.		
Dependent variable is 3-point scale for support of grizzly bear reintroduction in California.		

Table S11: Measuring Support for Reintroduction (Ordered Logit)

Variable	*B*	*SE B*	*Odds Ratio*
Species Awareness	0.02	0.09	1.02
Grizzly Existence (No)	-0.68***	0.23	0.50
Grizzly Existence (Don't Know)	-0.25	0.22	0.78
Benefits Component	1.78***	0.17	5.90
Costs Component	-0.61***	0.13	0.54
Altruism	0.35*	0.19	1.42
Biospherism	-0.18	0.15	0.84
Egosim	0.16	0.13	1.18
Recreation	-0.44***	0.08	0.64
Threat to Safety	0.15	0.101	1.16
Threat to Livelihood	-0.28***	0.10	0.75
Ideology	0.02	0.056	1.02
College Graduate	-0.22	0.18	0.80
Rural	0.10	0.12	1.10

Female	-0.27	0.21	0.76
Age	0.00	0.00	1.00
Income	0.04	0.05	1.04
White	0.11	0.19	1.12
Received Treatment	-0.11	0.17	0.90
AIC	1944.45		
N	754		

Intercepts:

	Value	***SE***	***T-value***
1|2	**-5.89**	**0.83**	**-7.12**
2|3	**-4.76**	**0.80**	**-5.95**
3|4	**-3.35**	**0.78**	**-4.29**
4|5	**-1.11**	**0.76**	**-1.45**
5|6	**0.07**	**0.76**	**0.09**
6|7	**2.15**	**0.77**	**2.79**

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. Dependent variable is 7-point scale for support of grizzly bear reintroduction in California.

Table S12: Collinearity Check (Model 3)

Variable	*B*	*SE B*
Constant	6.12***	0..26
Species Awareness	0.00	0.04
Grizzly Existence (No)	-0.32***	0.11
Grizzly Existence (Don't Know)	-0.15	0.10
Benefit Component	0.85***	0.06
Cost Component	-0.29***	0.06
Recreation	-0.26***	0.04
Threat to Safety	0.06	0.05
Threat to Livelihood	-0.16***	0.05
College Graduate	-0.06	0.09
Rural	-0.11	0.10
Female	0.00	0.09
Age	0.00	0.00
Income	0.02	0.02
White	0.13	0.09
Received Treatment	-0.05	0.08
R^2	.59	
N	761	

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. Dependent variable is 7-point scale for support of Grizzly bear reintroduction in California.

Table S13: Environmentalism Model (OLS)

Variable	*B*	*SE B*
Constant	6.33***	0.35
Species Awareness	0.01	0.04
Grizzly Existence (No)	-0.35***	0.11
Grizzly Existence (Don't Know)	-0.156	0.101
Benefit Component	0.87***	0.06
Cost Component	-0.32***	0.06
Environmentalism	-0.10*	0.05
Recreation	-0.26***	0.04
Threat to Safety	0.06	0.05
Threat to Livelihood	-0.13***	0.05
Ideology	-0.01	0.03
College Graduate	-0.08	0.09
Rural	0.01	0.06
Female	0.02	0.09
Age	-0.00	0.00
Income	0.02	0.02
White	0.10	0.10
Received Treatment	-0.02	0.09
R^2	.59	
N	761	

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. Ordinary least squares regression. Dependent variable is 7-point scale for support of grizzly bear reintroduction in California.

Table S14: Measuring Support for Reintroduction (Cost Index)

Variable	*B*	*SE B*
Constant	5.41***	0.64
Species Awareness	-0.00	0.04
Grizzly Existence (No)	-0.34***	0.11
Grizzly Existence (Don't Know)	-0.17	0.11
Benefit Component	0.92***	0.06
Cost Component	-0.23***	0.06
Altruism	0.21	0.13
Biospherism	-0.14	0.09
Egosim	0.08	0.06
Cost index	-0.11***	0.02
Ideology	0.01	0.03
College Graduate	-0.07	0.09
Rural	0.02	0.06
Female	-0.07	0.10
Age	-0.00	0.00
Income	0.02	0.02
White	0.08	0.10
Treatment	-0.02	0.09
R^2	.58	
N	764	

Note. *$p < .1$; **$p < .05$; ***$p < .01$.
Note. This is the same specification as Model 3, but with an index for cost statements.